A systematic and phylogenetic revision of the deep-sea genera *Anthothela* and *Primnoisis* (Coelenterata: Octocorallia: Alcyonacea) and an exploration of the biogeography of *Primnoisis*.

by

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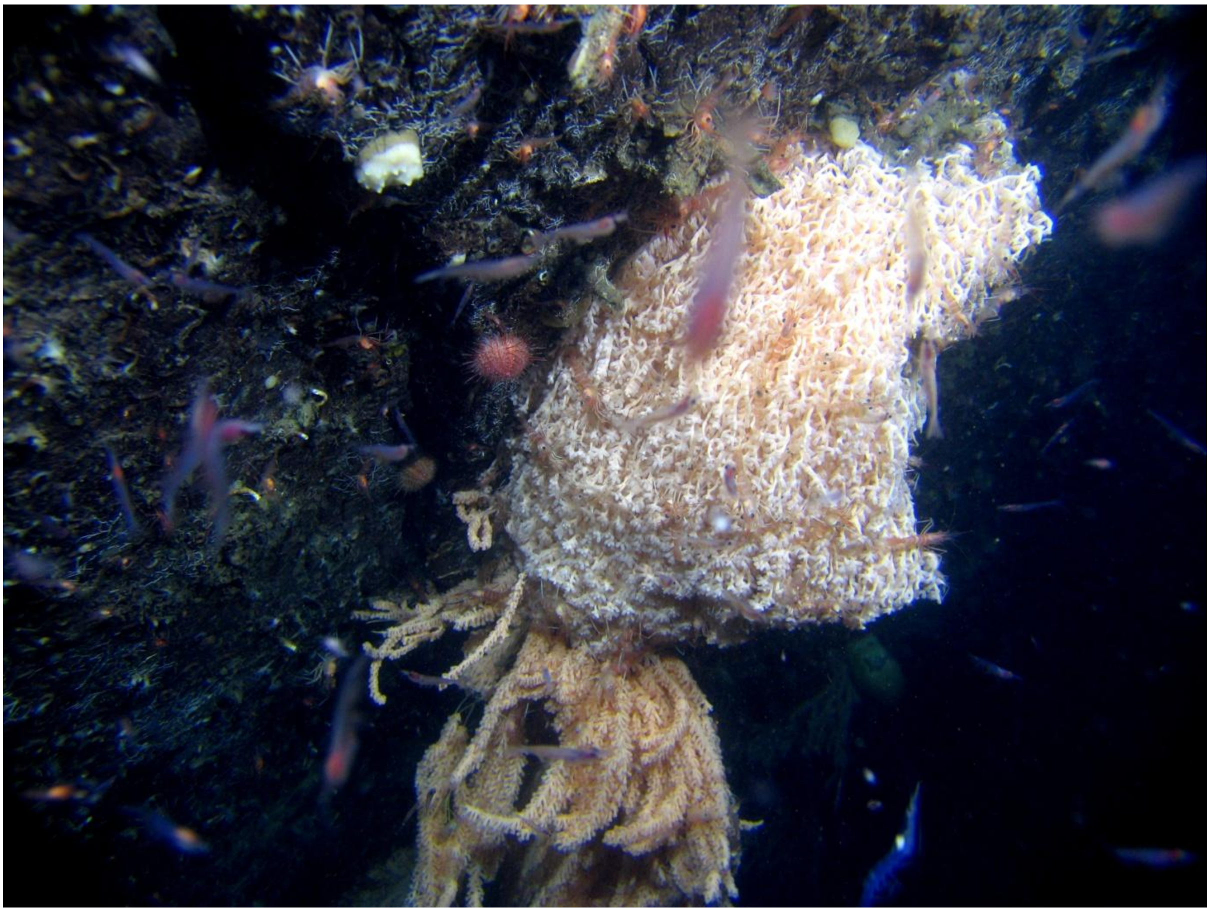
“Without taxonomy to give shape to the bricks, and systematics to tell us how to put them together, the house of biological science is a meaningless jumble.”

Robert May, 1990.

“We are astoundingly, sumptuously, radiantly ignorant of life beneath the seas….It's rather as if our first hand experience of the surface world were based on the work of five guys exploring on garden tractors after dark.”

Bill Bryson "A Short History of Nearly Everything", 2003.



Abstract

Octocorals have been recognised as abundant and ecologically significant on many deep-sea features. However their taxonomy and distribution remains poorly understood due to inadequate historical literature and a paucity of definitive morphological characteristics, and this is now hindering conservation and management in many of our important deep-sea marine ecosystems. For example, a decadal study of fishing impacts on seamounts south of Tasmania, Australia revealed a great diversity of octocorals, including two commonly collected and widely distributed genera, *Anthothela* and *Primnoisis*, but specimens could not be identified to species due to taxonomic confusion within the groups and hence could not be considered in diversity assessments and conservation measures. The taxonomy of these genera is revised herein in order to prescribe genus and species level morphological definitions, phylogeny and geographical extent. A multi-disciplinary approach was used combining morphological characteristics such as colonial branching patterns, polyp structure and sclerite form and arrangement, and phylogenetic reconstructions using two mitochondrial gene regions (mtMutS and igr1–COI).

Anthothela (Family Anthothelidae), with six nominal species globally, is here divided into four genera, two of which are new. *Anthothela* is found to have three valid species, *A. grandiflora, A. pacifica* and *A. tropicalis,* another species *Spongioderma* (?) *vickersi* is reassigned to *Anthothela* and two new species *A. aldersladei* and *A. quattriniae,* are described. *Anthothela argentea* and *A. nuttingi* are reassigned to *Victorgorgia* (Family Anthothelidae) and two new species of this genus, *V. eminens* and *V. nyahae* are described. These are the first records of *Anthothela* and *Victorgorgia* from Australia. One new genus, *Williamsius,* is described for *A. parviflora*, which is restricted to South African waters, and *Lateothela anitorkilda* n. gen., n. sp. is described to incorporate north Atlantic Ocean specimens which have been traditionally been mistaken for *A. grandiflora.* There was good congruence between morphological characteristics and molecular data at a generic level, but at the species-level morphological and genetic variation was very low. *Anthothela* and *Lateothela* n. gen. are found to be closely related to some nominal *Alcyonium* species and the Family Anthothelidae is shown to be paraphyletic.

The genus *Primnoisis* (Isididae) is retained with 7 of the 8 nominal species, *P. antarctica, P. rigida, P. ambigua, P. delicatula, P. fragilis, P. formosa, P. mimas*, validated and the eighth, *P. sparsa* is synonymised with *P. antarctica*. In addition, the species *Mopsea gracilis* is reassigned to *Primnoisis* and five new species are described; *P. chatham, P. erymna, P. millerae, P. niwa* and *P. tasmani*. Most of the species fell into two clear groups, defined both by morphology and genetics, for which two new sub-genera are proposed (*P.* (*Primnoisis*) and (*P. Delicatisis*)). Three species, *P. ambigua,* *P. mimas* and *P. tasmani* n. sp., could not be placed reliably in either sub-genus due to distinctive morphological features or genetic dissimilarity. It was not possible to confirm the monophyly of the genus due to unresolved relationships with the closely related genus *Notisis* and an undescribed Mopseinae genus. *P. tasmani* n. sp., with a distribution restricted to the southeast of Australia, is positioned basal to all other *Primnoisis* species based on DNA sequence data, suggesting southern Australia as the origin of the genus, with subsequent vicariant speciation after the separation of Gondwana and initiation of the Antarctic Circumpolar Current (ACC). North of the ACC, species are restricted to general geographical features such as seamount complexes, ridges and plateaus. Three species recorded south of the ACC are found to have extensive distributions around the Antarctic continental shelf and two further species appear to be widely distributed. *P. millerae* n. sp. is found to be separated by depth from other species on the Antarctic continental shelf and *P. fragilis* appears to have limited connectivity between vastly separated Antarctic populations, although low variability in the gene regions used and small sample size prohibit definitive conclusions.

These results illustrate significant undescribed diversity in the octocorals of the Southern Ocean and indicate that without comprehensive taxonomic reviews, current biodiversity estimates are likely to be grossly inaccurate, even at a genus level. This research will facilitate future ecological and conservation research on these octocorals by allowing more robust identification, and producing accurate geographic distributions and connectivity assessments. These in turn will guide conservation efforts to protect these poorly understood deep-sea communities.

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Abbreviations

AAD: Australian Antarctic Division, Hobart, Australia

AM: Australian Museum, Sydney, Australia

CMAR: CSIRO Marine and Atmospheric Research, Australia

CSIRO: Commonwealth Scientific and Industrial Research Organisation, Australia

IMAS: Institute for Marine and Antarctic Studies, Hobart, Australia

MAGNT: Museum and Art Gallery of Northern Territory, Darwin, Australia (collection code NTM)

MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, USA

MNHN: Muséum national d'Histoire naturelle, Paris, France

MOVI: Museu Oceanográfico do Vale do Itajaí, Brazil

MV: Museum Victoria, Melbourne, Australia

NIWA: National Institute of Water and Atmospheric Research, New Zealand

NHM: The Natural History Museum, London, United Kingdom (collection code NHMUK)

NHM,UIOslo: Natural History Museum, University of Oslo, Oslo, Norway

NHM Wein: Naturhistorische Museum, Vienna, Austria

NMNH: National Museum of Natural History, Washington DC, USA (collection code USNM)

NTNU-VM:Norwegian University of Science and Technology, University Museum,Trondheim, Norway

OMNZ: Otago Museum, Dunedin, New Zealand

SAMA: South Australian Museum, Adelaide, Australia

SIO: Scripps Institution of Oceanography, University of California, San Diego, USA

TMAG: Tasmanian Museum and Art Gallery, Hobart, Australia

UIB: University of Bergen, Bergen, Norway

UWMP: Uniwersytet Wroclawski, Muzeum Przyrodnicze, Warsaw, Poland (collection code MZW)

WAM: Western Australian Museum, Perth, Australia

YPM: Yale Peabody Museum of Natural History, Connecticut, USA

ZMA: Zoological Museum of Amsterdam, the Netherlands

ZMB: Museum für Naturkunde, Berlin, Germany

ZMUB: Zoological Museum of the University of Bergen, Norway

ZMUC: Zoological Museum of the University of Copenhagen, Denmark

Chapter 1. General Introduction.

1.1 Deep-sea Research

Deep ocean topographic features support diverse and elaborate ecosystems. The nature of the ecosystem varies with the topography which includes vast ocean plains, steep narrow canyons, sloping continental shelves and isolated seamounts. By coverage, they represent some of the most common ecosystems in the world, yet the deep ocean floor has remained largely unexplored despite much scientific endeavour (Brandt, De Broyer, et al. 2007; Danovaro et al. 2008). Parts of the fauna of the oceans and seas of the world have been studied for many years, originating with the landmark oceanographic voyages in the nineteenth century such as the *H.M.S. Challenger* expedition (Clarke, Aronson, Crame, Gili, & Blake 2004). The assemblages that were described and documented from these voyages often depended on available expertise and biases inherent in accessibility and sampling techniques. These limitations largely remain despite the development of novel techniques such as image analysis, sea floor mapping, submersibles and remotely operated vehicles (ROVs). The scientific community still relies heavily on simple yet destructive techniques of trawling the sea floor merely to collect and document the fauna at the most crude level (Etnoyer et al. 2006). As well as the damage incurred, the technique is recognised to have inherent difficulties such as under-sampling some faunal groups, damaging samples and masking variability within a trawl.

Similar to the sampling biases associated with trawling, currently available expertise for recognising and documenting the biodiversity and taxonomy of the deep-sea fauna unavoidably leads to subsets of relatively well understood faunal groups and others which remain poorly known with few experts. These sampling and knowledge biases have led to a patchiness of knowledge of the deep-sea fauna, compounded by geographic accessibility to existing hubs of science; those oceanic areas relatively close to population concentrations have been better studied than distant areas (Gutt, Sirenko, Smirnov, & Arntz 2004; Poore & Wilson 1993). Recent advances in new technologies (e.g. AUVs, ROVs and submersibles) have greatly increased opportunities to observe taxa in situ and collect targeted specimens with minimal damage, and have facilitated an expanded recognition and knowledge of the diversity, significance, ecology, evolution and uniqueness of deep-sea communities (Doughty, Quattrini, & Cordes 2014; Long & Baco 2014; Shank 2010; Thresher et al. 2014). However, these technologies have in turn meant an increase in fishing pressures and long-term anthropogenic impacts, and our understanding of the ability for communities to recover is limited (Miller, Williams, Rowden, Knowles, & Dunshea 2010; A. Williams et al. 2010).

1.2 Benthic fauna of the Southern Ocean

The Southern Ocean is recognised as one of the world’s five oceans. It encircles the Antarctic continent extending north to 60°S, although the northern boundary is disputed by some countries. Currently, the Southern Ocean is understood by most countries to be all waters south of the mean position of the Antarctic polar front (historically known as the Antarctic Convergence) (Clarke, Griffiths, Linse, Barnes, & Crame 2007). The polar front is where the cold waters of the Antarctic meet the warmer waters of the large oceans and is usually between 48° to 61° south (Brandt 2005). The position of the polar front moves around seasonally so at various stages some subantarctic islands have been considered within and outside the polar front. For political purposes, the Australian Government defines the Southern Ocean to be anything south of the main continent of Australia and the island of Tasmania starting at roughly between 35° to 45° south (Darby 2003).

The Southern Ocean has distinctive features such as a relatively deep continental shelf, stable low temperatures and a fast flowing easterly current, the Antarctic Circumpolar Current (ACC) which forms an oceanographic barrier between the Southern Ocean and adjacent water bodies (Barnes, Hodgson, Convey, Allen, & Clarke 2006; Brandt, De Broyer, et al. 2007). These features combine to result in a unique and diverse benthic community. In particular, benthic fauna on the Antarctic continental shelf are diverse, isolated and strikingly distinct due to the absence of skeleton-breaking (durophagous) predators such as crabs, the relatively deep continental shelf, the effective isolation from northern waters due to strong water flow of the ACC and the impacts of iceberg scour (Brandt 2005; Clarke et al. 2004; Clarke, Griffiths, et al. 2007; Clarke & Johnston 2003) but much of the biodiversity of parts of this ocean remains undescribed, particularly key habitat-forming benthic groups such as sponges, hydroids and corals (Brandt, De Broyer, et al. 2007). Compared to equivalent deep-water habitats elsewhere, Southern Ocean benthic communities appear to have a significantly higher percentage of suspension feeding, complex epifaunal groups (Clarke et al. 2004; Gili, Coma, Orejas, López-González, & Zabala 2001; Orejas et al. 2000). Some communities are relatively well understood in areas around the Antarctic Peninsula, the Ross Sea and the East Weddell Sea (Arntz et al. 2005; Brandt, De Broyer, et al. 2007; Clarke et al. 2004; Clarke, Griffiths, et al. 2007; Griffiths, Barnes, & Linse 2009). However, the composition of benthic communities from the east Antarctic continental shelf and the relationship with the fauna from the west Antarctic has been largely assumed or simply estimated (Janosik & Halanych 2010).

The ACC is thought to isolate the ecosystems on the Antarctic continental shelf from the shelf fauna of southern African, American and Australian continents (Arntz et al. 2005; Brandt 2005; Griffiths et al. 2009; Pierrat, Saucède, Brayard, & David 2013). Larval dispersal eastwards around Antarctica, mediated by the strong ACC, has lead to the expectation that many Southern Ocean species will have a circumpolar distribution. However, for many fauna there has been insufficient sampling to confirm or refute this assumption. Most sampling has been centred around Antarctic stations resulting in patch sampling, disjunct records and only the assumption that species occur at sites in between. Recently there is increasing evidence of cryptic speciation within nominal species with a presumed 'circumpolar' distribution, across a wide variety of taxa including echinoderms, molluscs and crustaceans (Allcock et al. 2011; Baird, Miller, & Stark 2011; Hunter & Halanych 2010; Krabbe, Leese, Mayer, Tollrian, & Held 2010; Wilson, Hunter, Lockhart, & Halanych 2007; Wilson, Schrödl, & Halanych 2009). Clarke et al. (2007), using the relatively well known molluscan fauna, found surprisingly few taxa with circumpolar distributions. Additionally, for shallow water benthos, local conditions such as eddies and iceberg movement appear to be more influential on distribution than the ACC (Gutt & Piepenburg 2003; Raguá-Gil, Gutt, Clarke, & Arntz 2004).

Antarctic biological communities are considered central to global processes, including driving nutrient rich bottom water and diversity radiations (Brandt, De Broyer, et al. 2007). High algal productivity in the austral summer under the sea ice feeds into the Antarctic Bottom Water (ABW) mass which flows across the abyssal plains connecting the Southern Ocean to other oceans at great depth (Brandt 2005). The Antarctic continental shelf is relatively deep and the often eurybathic Southern Ocean deep-sea fauna are thought to be able to migrate across the abyssal plains of the Southern Ocean (Brandt, De Broyer, et al. 2007). Invertebrates groups such as polychaetes, molluscs, pycnogonids, amphipods and isopods are highly diverse in Antarctic benthos possibly due to the diversification and allopatric speciation caused by isolation and population disjunction during glacial cycles (Thatje, Hillenbrand, & Larter 2005; Wilson et al. 2009). Some groups are thought to have undergone a radiation with submergence from the Antarctic continental shelf into the deep ocean basins with the ABW although this is not consistent even within faunal group (Arntz et al. 2005; Brandt 2005; Brandt, De Broyer, et al. 2007; Griffiths, Arango, Munilla, & McInnes 2011). The benthic communities found at the subantarctic islands have been recognised as functional stepping-stones between the Antarctic continental shelf and northern habitats, and biodiversity studies are elucidating the links and evolutionary origin of the Antarctic benthic fauna (Arntz et al. 2005; Arntz et al. 2006; Fraser, Nikula, Spencer, & Waters 2009; Griffiths et al. 2011; Gutt, Fricke, Teixidó, Potthoff, & Arntz 2006; O'Loughlin, Paulay, Davey, & Michonneau 2013; Rogers 2007). While the western peninsula regions of the Antarctic continent are experiencing some of the most rapid climate change on Earth (Clarke, Murphy, et al. 2007) the likely effects of climate change on Antarctic benthic communities, their distributions and concomitant effects on global processes are largely unknown.

1.3 Octocorallia

Within the Phylum Cnidaria, the Class Anthozoa is defined as those cnidarians which have only benthic life cycles. This class consists of two subclasses, Octocorallia and Hexacorallia (Daly et al. 2007), with Octocorallia unified by the occurrence of eight tentacles around the oral cavity of each polyp. Commonly known as octocorals or soft corals, Octocorallia are sedentary, suspension feeding colonies of polyps which form a common and important part of the ecosystems of basically all benthic marine systems at all depths (Fabricius & Alderslade 2001; Orejas et al. 2002). Octocorals can form dense beds of complex and intricate habitat which, as well as a being an inherent part of the diversity and biomass of these communities, provide shelter and ecological niches for many species (Andrews et al. 2002; Koslow et al. 2001; Krieger & Wing 2002; Mosher & Watling 2009; Quattrini, Ross, Carlson, & Nizinski 2012). Most octocorals require hard substrate for anchorage thus they often have distributions restricted to seamounts and other topographical features such as canyons and continental slopes. Not only are these the areas where fishing effort can be concentrated but seamounts and canyons can be great distances apart and the degree of connectivity between many of these habitats is not well understood (Baco & Cairns 2012; Cho & Shank 2010; Koslow et al. 2001; Miller et al. 2010; Richer de Forges, Koslow, & Poore 2000; Shank 2010)**.** Octocorals are often upright and brittle and thus likely to be severely affected by benthic trawling (Althaus et al. 2009; Andrews et al. 2002; Clark & Rowden 2009; Koslow et al. 2001; A. Williams et al. 2010). Additionally, the deep-water colonies can have a highly patchy but locally dense distribution (Orejas et al. 2002) so a single benthic trawl may damage or destroy many octocoral colonies. They are understood to have a relatively slow recovery potential due to slow growth and limited dispersal ability (Althaus et al. 2009; Andrews et al. 2002; Grigg 1988). A review of the known reproductive traits of octocorals found approximately 50% of species were broadcast spawners and 50% were brooders, but this study admits the results are based mainly on shallow water taxa (Kahng, Benayahu, & Lasker 2011). The life history of deep-sea octocorals has been rarely studied but some species have been shown to brood and there are possibly short larval life spans for others (Bayer 1996; Orejas, Gili, López-González, Hasemann, & Arntz 2007; Orejas et al. 2002). Combinations of these characteristics mean a high degree of endemism and a different species composition for each community could be expected (France & Hoover 2002; Koslow et al. 2001; Richer de Forges et al. 2000) as these characteristics affect the ability of a species to colonise a new habitat, especially an isolated one.

1.4 Southern Ocean Octocorallia

The Octocorallia fauna of the Southern Ocean has been explored by various expeditions and voyages over the last two centuries (e.g. Broch 1965; Grant 1976; Hickson 1907; Kükenthal 1912; Kükenthal

1919; J. A. Thomson & Rennet 1931; Wright & Studer 1889). Kükenthal (1919) summarised the world-wide knowledge of Octocorallia of the time, including distributions and species lists. Substantial research has continued since then but has been hampered by irregular sampling opportunities, especially in the Southern Ocean, and inadequate literature. The knowledge of the Octocorallia fauna in the regions south of Australia and New Zealand is particularly patchy and poorly documented with most of the Octocorallia fauna of these areas not being reviewed or updated for many years (Alderslade, Althaus, McEnnulty, Gowlett-Holmes, & Williams 2014). There were a number of research expeditions in the past which collected many of the known species of the area but the descriptions are often brief, inadequate and lack drawings or pictures (McFadden in Daly et al. 2007; Grant 1976; Gravier 1913; Roule 1908; Studer 1878; J. A. Thomson & Rennet 1931). It is thus extremely difficult to be confident of identification of new specimens without comparing with the type specimens, which are often housed in northern hemisphere museums and sometimes lost altogether.

Modern techniques of taxonomy and systematics allow substantial changes to the approach and methods of biodiversity research and faunal relationships (McFadden, Alderslade, van Ofwegen, Johnsen, & Rusmevichientong 2006). Molecular analysis has become a fundamental part of species differentiation, phylogenetic and phylogeographic research in many phyla (Álvarez & Wendel 2003; Shearer, van Oppen, Romano, & Wörheide 2002) while microscope photography, and fast and easy sharing of photographs and descriptions across the world, have greatly improved taxonomic research and collaboration. Currently there is substantial interest in the Octocorallia fauna of the Antarctic continent with international scientists researching some of the most common groups found around Antarctica, but with a highly biased focus on the Antarctic Peninsula (e.g. Cairns 2002; López-González 2005; López-González & Gili 2001, 2005; López-González & Williams 2002; Orejas et al. 2007; Taylor, Cairns, Agnew, & Rogers 2013; G. C. Williams & López-González 2005; Zapata-Guardiola & López-González 2009, 2010b). Most of these studies have focussed on reviewing the taxonomy and systematics of taxa with minimal investigation of distributions, connectivity or population structure. The area south of Australia and New Zealand which encompasses East Antarctica is relatively poorly studied for octocorals (Alderslade et al. 2014) but is of interest to many researchers, especially those addressing biogeographic questions, and research completed here will form a critical part of the overall knowledge of the Southern Ocean octocorals.

1.5 Octocorallia systematics

Existing research on the higher order phylogenetic relationships of the subclass Octocorallia is substantial (Berntson, Bayer, McArthur, & France 2001; Daly et al. 2007; McFadden, France, Sánchez, & Alderslade 2006; McFadden, Sánchez, & France 2010; Sánchez, McFadden, France, &

Lasker 2003; Won, Rho, & Song 2001). While the subclass, Octocorallia has consistently been shown to be monophyletic (Berntson, France, & Mullineaux 1999; McFadden in Daly et al. 2007; Won et al. 2001), the lower-level divisions within Octocorallia are more problematic. Definitions of orders and suborders have been changed a number of times and there is no general consensus on a robust framework (McFadden et al. 2010). However, currently there is agreement on three orders for functionality: Pennatulacea (sea pens); Helioporacea (blue corals); and the largest Alcyonacea (soft corals and gorgonians) (Bayer 1981; McFadden in Daly et al. 2007; Fabricius & Alderslade 2001). The Alcyonacea includes 34 families and approximately 3000 extant species (Breedy, van Ofwegen, & Vargas 2012; McFadden inDaly et al. 2007; McFadden & van Ofwegen 2012c, 2013; van Ofwegen & McFadden 2010; G. C. Williams & Cairns 2013), although so many of the families and genera need revision that these estimates are highly fluid (McFadden in Daly et al. 2007).

Octocoral morphological characteristics have historically been based around colony shape such as presence and structure of axes, branching architecture, polyp arrangement and form, and the presence, shape and arrangement of sclerites in the outer and inner tissue layers (Bayer 1981; Bayer, Grasshoff, & Verseveldt 1983; Fabricius & Alderslade 2001). These characters are used in combination for taxonomic decisions but can often occur on a continuum making some degree of subjectiveness in the decisions always necessary especially with phenotypic plasticity and intra-individual variability (Prada, Schizas, & Yoshioka 2008; Sánchez, Aguilar, Dorado, & Manrique 2007; West, Harvell, & Walls 1993).

Compared with higher order animals, mitochondrial nucleotide sequences are highly conserved in anthozoans (Concepcion, Crepeau, Wagner, Kahng, & Toonen 2008; France & Hoover 2002; Hellberg 2006; McFadden et al. 2011; Shearer et al. 2002) so it has been difficult to interpret inter-specific versus intra-specific boundaries using the classic mitochondrial genetic sequences, specifically those regions usually used for 'barcoding' (McFadden et al. 2011). Phylogenetic and biodiversity analyses have been conducted using many sequences of the octocoral genome: e.g. 16S rRNA (France & Hoover 2002; Sánchez, Lasker, & Taylor 2003; Smith, McVeagh, Mingoia, & France 2004); 18S rDNA (Berntson et al. 1999; Pante et al. 2012; Won et al. 2001); 28S rDNA (McFadden, Brown, Brayton, Hunt, & van Ofwegen 2014; Reijnen, McFadden, Hermanlimianto, & van Ofwegen 2013); COI (Alderslade & McFadden 2011; France & Hoover 2002); ND2, ND6 (Baco & Cairns 2012; Herrera, Baco, & Sánchez 2010; McFadden, Tullis, Hutchinson, Winner, & Sohm 2004); but the most commonly used marker is a mitochondrial region originally known as msh1 (McFadden et al. 2010) and now known as mtMutS (Bilewitch & Degnan 2011). The mtMutS gene region, originally found by Pont-Kingdon et al. (1995) (and called msh1) appears to be specific to octocorals and universally present in all octocorals sequenced to date. This region is likely to have resulted from a horizontal gene transfer into the mitochondrial genome of the octocoral ancestor after divergence from other anthozoans, and is assumed to be involved in repair of replication errors in the mitochondrial DNA, thus slowing the rate of mutation and genetic change within the octocoral mitochondrial genome (Bilewitch & Degnan 2011; Pont-Kingdon et al. 1998). Even though it has this role in DNA mismatch repair, the mtMutS region is generally recognised as the most variable of the mitochondrial markers commonly used for phylogenetic reconstruction in octocorals (Baco & Cairns 2012; McFadden et al. 2011) although it has limitations to certain genera and is not always variable enough to distinguish between species (Cairns & Bayer 2005; Concepcion et al. 2008; McFadden, Alderslade, et al. 2006).

Other gene regions have shown promise for octocoral systematics. Concepcion et al. (2008) found sufficient difference in a nuclear gene region called SRP54 to distinguish between visually different colonies of *Carijoa riisei* when the mtDNA region ND2 and morphological analysis of sclerites did not. Additionally, Stemmer et al. (2013) found this gene region to be 10x more variable than the mitochondrial gene region ND6/ND3 in xeniid octocorals. This supports Hellberg (2006) who found that the anthozoan mitochondrial genome has approximately 100 time slower rates of substitution than other metazoans while the nuclear genes tended to have higher rates of polymorphisms and variability than other animals. However, subsequent studies have failed to reliably amplify this particular nuclear gene region in other octocoral species (Baco & Cairns 2012; McFadden et al. 2011; Pante et al. 2012) or if amplified could not be reliably aligned for use in phylogenetic analysis (Watling & France 2011). The nuclear gene region ITS has been found to be informative for many corals, especially when secondary structures are included (Aguilar & Sánchez 2007; Herrera, Shank, & Sánchez 2012) however it has also often found to present multiple copies (intraindividual polypmorphisms) (Baco & Cairns 2012; Dueñas & Sánchez 2009; McFadden, Donahue, Hadland, & Weston 2001) which confounds data analysis and interpretation. Recent research on microsatellites (Porto-Hannes & Lasker 2013; Smilansky & Lasker 2014), assessments of genetic distance thresholds (McFadden, Brown, et al. 2014), single nucleotide polymorphisms (SNPs) or character-based analyses (McFadden et al. 2011), haplotype distributions (Baco & Cairns 2012; Pante et al. 2012) and mitochondrial gene orders (Figueroa & Baco 2014; Pante, Heestand Saucier, & France 2013; Uda et al. 2013) have advanced knowledge of octocoral diversity and species boundaries, and next-generation sequencing has great potential for future phylogenetic research (Reitzel, Herrera, Layden, Martindale, & Shank 2013).

Neither morphological differences nor molecular analyses alone have proved consistent and predictable enough to create robust higher order phylogenies or repeatable lower level population assessments. Combining phylogenies both from morphological and molecular approaches should allow a greater reliability and clarity, especially if the molecular data can assist in highlighting morphological characteristics which correspond to monophyletic groups (France 2007; McFadden, Alderslade, et al. 2006). In addition, quantitative research on numerically measurable morphometric characteristics can further assist in establishing inter- and intra-species boundaries (Miller 1994; Pante & Watling 2012).

1.6 Thesis objective and outline

The objective of this thesis was to revise and clarify the taxonomic validity, phylogenetic position and internal species relationships of two common Octocorallia genera from the Southern Ocean, *Anthothela* (Sars, 1856) and *Primnoisis* Studer [& Wright], 1887. These two genera were chosen due to the abundant number of specimens available, particularly from the seamounts south of Tasmania, despite neither genus previously being recorded from Australian waters. Additionally, most of the specimens could not be reliably placed in existing species due to inadequate descriptions indicating the need for a taxonomic revision of those genera. The taxonomic and phylogenetic position of both genera and the species within has been obscure, being based on old and inadequate descriptions, and species boundaries have been too poorly defined to be used for species identification making the taxa unavailable for biodiversity assessments. In addition, biogeographic analyses including species distribution data and population connectivity were used to understand the likely origins and evolution of the genus *Primnoisis* in the Southern Ocean. In combination, these data will provide clear taxonomic criteria to inform future biodiversity assessments, for example in the designation of Marine Protected Areas, will inform distribution analysis and connectivity estimations, and illumination of how these corals may have evolved, radiated and adapted in the past will help guide management and conservation of deep-sea benthos as the climate changes.

Chapter 2 focuses on the genus *Anthothela* which has previously been recorded in deep waters from the Atlantic, Pacific and Indian Oceans but samples collected from the seamounts south of Tasmania constituted the first record of the genus from Australian waters. In these recent collections specimens were large, colourful and numerous making them a useful marker taxa on video analyses but the taxonomic confusion was such that the specimens could not be reliably identified. The chapter is a taxonomic review of the genus *Anthothela* and related taxa, using both morphological descriptions and phylogenetic reconstructions from two mitochondrial gene regions in combination to redefine the boundaries of *Anthothela*, investigate the validity of nominal species and determine the relationship of the specimens collected locally with specimens collected globally.

Chapter 3 focuses on the genus *Primnoisis* which has previously been recorded mainly in Antarctic and subantarctic waters so numerous specimens collected from the seamounts of Tasmania and Macquarie Ridge presented an unexplored possible connection between the faunas. While the genus definition was reasonably robust, the species within were inadequately defined for any species-level assessment. A multidisciplinary approach, combining morphological characteristics and two mitochondrial gene regions, was used to taxonomically review the genus including the prescription of species definitions and the assessment of phylogenetic relationships within the genus and with closely related taxa.

The strong ACC is expected to act as an oceanographic barrier to the movement of many taxa, as well as an aid to extensive distributions around the Antarctic continental shelf, hence the presence of *Primnoisis* either side of the current and apparent circumpolar distributions presented the opportunity to explore the connectivity and origin of these populations using collated distribution data and phylogenetic analysis (Chapter 4). Additionally depth stratification of *Primnoisis* species both north and south of the ACC was examined as depth is increasingly recognised as an important influence on population structuring.

In Chapter 5, the efficacy and application of the multi-disciplinary approach to taxonomy is discussed along with the restrictions and difficulties still present in octocoral systematics research. The difficulties inherent in species level delineation in octocorals and the future possibility of effective character-based genetic analysis (or SNP comparisons) is explored, as are the broad implications of the biogeographical patterns identified for *Primnoisis*.

Chapter 2. A taxonomic revision of the genus *Anthothela* (Alcyonacea: Anthothelidae) and associated genera using morphological and molecular data.

2.1 Introduction

2.1.1 Systematic position of *Anthothela* Verrill, 1879

The genus *Anthothela* is recognised as part of the subordinal group Scleraxonia, within the order Alcyonacea and the family Anthothelidae. Scleraxonian octocorals are grouped by similarities in morphological structure but they are not considered a true monophyletic suborder (Daly et al. 2007; Fabricius & Alderslade 2001; McFadden, France, et al. 2006; McFadden et al. 2010). The subordinal grouping is composed of seven families, some of which, like Anthothelidae, are characterised by the presence of an axis composed of sclerites pressed tightly together called a medulla and an external surface layer called a cortex. Other families vary from this, some with fused sclerites in the axis and others lacking an axis. Many familial and generic groupings require major revision and rearrangement, ideally using a combination of morphology characteristics and molecular phylogenetics (Daly et al. 2007).

Anthothela is a genus believed to be widespread in deep waters, for example, the Smithsonian National Museum of Natural History collection has 103 registered specimens from the north and south Pacific Ocean, north and south Atlantic Ocean and the Antarctic Ocean (accessed June 2014). Over the years a variety of specimens have been assigned to it causing considerable confusion regarding the defining characteristics and a widening definition (Bayer 1956, 1961; Kükenthal 1919; Studer 1894; G. C. Williams 1992a). This appears to have resulted in true *Anthothela* colonies being incorrectly assigned, colonies being erroneously assigned to *Anthothela*, and species mistakenly erected to accommodate membranous forms of *Anthothela*. One of the most notable characteristics observed in the genus is the ability of colonies to grow both in a membranous and a branching form, often in a single colony (Kükenthal 1924; Molander 1929). In the presence of a medulla an *Anthothela* specimen was historically thought to be relatively easily recognised. However, a colony which has not (yet?) grown a medulla may easily be mistaken for other genera outside the Scleraxonia, such as some of the nominal *Clavularia* species which have similar polyp and sclerite morphology (Molander 1929). Additionally, it is becoming increasingly accepted that axis morphology may not be a definitive phylogenetic characteristic; for example within the scleraxonian informal subordinal grouping the axial medulla appears to have evolved a number of times

(McFadden, France, et al. 2006; Sánchez, Lasker, et al. 2003). The family Anthothelidae was originally erected based on morphological features of the axial medulla and coelenteric canal arrangement and now requires revision as do many of the genera (López-González & Briand 2002; McFadden, France, et al. 2006).

Currently there are seven recognised species of *Anthothela: A. grandiflora* (Sars, 1956); *A. argentea* Studer, 1894; *A. macrocalyx* (Nutting, 1911); *A. pacifica* Kükenthal, 1913; *A. parviflora* Thomson; 1916; *A. nuttingi* Bayer, 1956; and *A. tropicalis* Bayer, 1961. Existing records of *A. grandiflora* suggest it is widespread in the northern Atlantic but most of the other *Anthothela* species have been established from single or sparse records only. All species appear restricted to deep water.

2.1.2 The taxonomic history of the genus *Anthothela*

The first known record was a specimen collected from "Öxfjord i Finmark" in Norway, which was described and assigned the name *Briareum grandiflorum* by Sars (1856). It was described as a large, rather tangled mass of firm, basically cylindrical, slender branches with polyps irregularly dispersed all over the colony, although they were often quite crowded around the tips of the branches. The colony had no main stem, all the branches being approximately the same size, and there was evidence of anastomoses with neighbouring branches. Sars emphasised the "extraordinairement grandes" (extraordinarily large) size of the polyps as one of the main distinguishing features along with the short polyp body cavities ending abruptly at the spongy, sclerite-filled medulla , thus separating the specimen from the Alcyoniidae despite the similar appearance of the polyps. Indeed, the short body cavity truncating at the scleritic medulla appears to be what led Sars to assign the specimen to *Briareum* (F: Briareidae). There is mention of a spreading or membranous component of the colony in the description although most of the colony consisted of narrow, tangled branches. The sclerites were described as universally narrow, tuberculate spindles in both the cortex and the medulla, and also on the polyps. Sars stated the polyps were connected via fine canals in the cortex but did not specifically discuss the longitudinal boundary canals around the medulla which would later become one of the defining characteristics of the family Anthothelidae.

Other researchers commonly found similar colonies from fjords around Norway and assigned them to *Briareum grandiflorum,* (Sars 1857; Storm 1879b; 1892) although at one stage some specimens were recorded as *Paragorgia grandiflora* (Storm 1879a). This name change was not explained and was not adopted by later workers. Similar specimens were collected from the north-west Atlantic, close to the US coast, which prompted Verrill (1879a) to establish a new genus, *Anthothela,* to encompass *Briareum grandiflorum* and "allied species". The main characteristic used by Verrill to differentiate *Anthothela* from *Briareum* and *Paragorgia* was that the "polyp-cells are prominent and permanently exsert, and the polyps themselves are not entirely retractile". He also mentioned the ability of a colony to grow as an encrusting form as well as producing upright branches. In a preliminary list, Verrill (1879b) nominated a second species (*A. insignis*) without a description but subsequently synonymised it with *A. grandiflora* (Verrill 1883). Studer (1887) addressed the systematics of the family Briareidae, recognising two subfamilies differentiated by the presence (Briareinae) or absence (Spongioderminae) of nutrient canals in the medulla. *Anthothela* was placed in Briareinae due to a low number of indistinct longitudinal channels extending through the medulla along with solenia in the cortex connecting the polyp bodies.

In his later paper, Verrill (1883:40) described the sclerites as tuberculate spindles of various thickness and length. He also stated in the revised genus diagnosis that the "calicles [are] prominent, not capable of being contracted within the coenenchyma" without mentioning whether or not the polyps are retractile within these calyces. This was interpreted later by Broch (1912b) as a profound difference from the original definition of the genus; he suggested Verrill realised that the polyps can invaginate within the calyx and thus the statement "not entirely retractile" should be removed from the definition of the genus. Grieg (1894) also clearly stated that "polypis non retractiibus" should be removed from the generic diagnosis as many of the colonies stored in the Bergen Museum have polyps retracted into an obvious calyx. Despite these assertions regarding the change in the definition of the genus, confusion still remained over the retractile or non-retractile nature of the polyps and this continued to feature as an unwarranted defining characteristic of the genus for many years. Grieg (1894) stressed while the polyps are retractile into the calyces, the presence of an obvious calyx which cannot retract into the surrounding coenenchyme is the characteristic he explicitly used to distinguish *Anthothela* from *Briareum* while the absence of dimorphic zooids distinguished it from *Paragorgia.*

An additional species was added to *Anthothela* by Studer (1894), obtained from the dredging operations carried out by the US Fish Commission Steamer "Albatross" along the eastern coast of the Pacific Ocean. The specimen, given the name *A. argentea* due to the glassy or silvery colour of the sclerites, was described as having a main trunk, from which the slender branches occur at right angles and the sclerites were described as clubs and prickly, bent spindles. No diagrams accompany the unfortunately brief description. A central trunk is a different growth form to that described by Sars in the original description of *A. grandiflora* where he specifies there is no central stem or predictable growth pattern, thus the inclusion of this species necessarily expanded the genus definition. The species was relegated to "Zweifelhafte" (doubtful) by Kükenthal (1916, 1919, 1924) on the basis of the inadequate description and it has not been re-described since.

The apparent distribution of *Anthothela grandiflora* continued to expand with samples collected from waters off the east coast of Mexico through to Newfoundland. It was considered "common off

Nova Scotia" (Verrill 1885) and was found throughout Norwegian waters (Grieg 1891; 1894; Storm 1892; 1896; Whiteaves 1901). Broch (1912b) provided a very detailed description of specimens from Norway including the holotype of *A. grandiflora.* This was a seminal description, often referred to by future researchers, perhaps more than the original description by Sars. Unfortunately, it now appears that Broch had specimens from different genera and thus he unwittingly introduced significant confusion into what defines *Anthothela,* including variations in colony colour and form and predominant sclerite types; for example Verrill (1883) stated the colonies are "in life, pale yellow or buff" and the sclerites were all tuberculate spindles of various thickness and length while Broch described the colour as bright rose-red or pale brownish and short, warty rodlets as being abundant in the calyces and cortex.

Molander (1915) declared *Clavularia alba* (=*Rhizoxenia alba*) (Grieg, 1887) to be "among *A. grandiflora*", claiming "complete resemblance", only to rescind this decision three years later (Molander 1918b) where he declared it to be a version of *Gersemia fruticosa* (Sars, 1860). Later he again suggested it belonged in *Anthothela* as a membranous form (Molander 1929), taking the binomial *Anthothela alba* (Grieg, 1887). While discussing species thought to be exclusively membranous Molander (1918c) supported Broch's (1912b) observation that *A. grandiflora* can form substantial membranous-only colonies, although admitting that it can form large colonies with complex branching. In this paper, he also claimed that it had substantial resemblance to two membranous species *Anthelia borealis* (=*Clavularia borealis*) (Koren & Danielessen, 1883) and *Anthelia fallax* Broch, 1912, particularly in the size and form of the sclerites. He suggested that as these sclerite variations were, in his opinion, the only notable difference between these species and *A. grandiflora* they should be considered variations of the latter species thus becoming *A. grandiflora* var. *borealis* and *A. grandiflora* var. *fallax.* This is later refuted and disregarded by other researchers (Broch 1935; Madsen 1944).

A new family, Anthothelidae, was created by Broch (1916) but, other than *Anthothela* and a new genus he described (*Suberiopsis* Broch, 1916), he did not specify which genera were to be placed in the new family. He did indicate however, that genera with coelenteric canals penetrating the medulla were to be in a subfamily Anthothelinae, and those without in the subfamily Spongioderminae. He argued the family differed from Briareidae by the polyp body truncating at the medulla rather than continuing into the medulla and by the presence of a ring of longitudinal canals surrounding the medulla which separates the medulla from the cortex. Broch also described some canals running longitudinally through the central medulla in older parts of a colony and horny sheaths around the thorny sclerites.

Later, Kükenthal (1916, 1919, 1924) retained Broch's description of the colour of *A. grandiflora* and perpetuated much of his description but did not accept the familial division due to a disagreement regarding the placement of *Briareum* and *Paragorgia.* Kükenthal was not sure that the polyp body cavities extended into the medulla in those genera thus, in his opinion, making the distinction between the two families untenable. In his "System und Stammesgeschichte der Scleraxonier und der Ursprung der Holaxonier" Kükenthal (1916) provided a key which separated *Anthothela* from the other genera in the subfamily Briareinae with the assertion that the polyps only occur on one side of the branches. This was in complete contradiction to Sars' original description which stated that the polyps were placed without order and were dispersed around the branches. Later Kükenthal (1919, 1924) admitted that the arrangement of polyps was without pattern in larger colonies and his key to the genera of the Briareidae did not mention the arrangement of polyps but differentiated *Anthothela* by the presence or absence of anastomoses.

In 1922 Verrill reassessed the genus which he had established 37 years before, following Kükenthal in retaining the genus in the Briareidae, but he did not add significantly to any consensus on diagnostic characteristics of the genus. In fact he may have made the same error as Broch (1912b) by mixing specimens of two genera in his description of *A. grandiflora* (Verrill 1922) [see Remarks after description of *A. grandiflora* within].

Thomson (1927) did not recognise the family Anthothelidae either when he published descriptions and superb figures of colonies he identified as *A. grandiflora* collected off the coast of Portugal and Spain. This expanded the apparent distribution of the species. All four colonies were from over 1000m deep and three were portrayed in the figures as cream to yellow and one colony as purple. Thus the live colour of *A. grandiflora* had, by then, been described or depicted as yellow or buff, rose-red or pale brownish and purple. Deichman (1936) included *Anthothela* in a key to the Briareidae which follows Kükenthal's (1919) distinction based on common anastomoses.

Stiasny (1937) mentioned two colony forms in specimens he identified as *A. grandiflora*. The first form has a flat membranous plate from which robust, upright stems with little or no anastomoses arise, while the description of the colony form of the second specimen more closely matches the original description of *A. grandiflora* (dense shrub with many anastomoses and bifurcations). Stiasny expanded the diagnosis of *Anthothela* to include the different colony forms and discussed the arrangement of the medullary canals, retaining *Anthothela* in Briareidae but with some reservation. Verseveldt (1940) later investigated the same specimens but did not mention the two colony forms. He re-established the family Anthothelidae, clarifying the importance of the circle of longitudinal canals, separating the cortex from the medulla, the truncation of the polyp gastric cavity at the medulla and the lack or near lack of canals in the central medulla. For *Anthothela,* he specifically proposed “boundary space” rather than boundary canals for the gap separating the medulla and cortex. He argued the cortex was only connected by “thin and short columellae” which were actually the reduced partition walls of the boundary canals present in “other genera” and that the canals are basically “solenia, fused into one space”. He disagreed with Stiasny’s claim that there are two layers to the cortex and he dismissed Stiasny’s diagram depicting central medulla canals in the upper part of a colony. He also rejected the claim by Broch (1912b), Molander (1918c) and Kükenthal (1919) that in *A. grandiflora* the medulla is not distinctly separated from the cortex.

Verseveldt (1942) re-assigned *Semperina (Suberia) macrocalyx* (Nutting, 1911) to the genus. This specimen had been collected by the Siboga Expedition in deep waters off the coast of Indonesia, and therefore significantly extended the known distribution of *Anthothela*. The main difference to *A. grandiflora* is the presence, in *A. macrocalyx,* of large, club-shaped, closely warted sclerites lying longitudinally on the backs of the tentacles which, although not noted by Nutting (1911), were described and figured by Thomson and Dean (1931), Stiasny (1937) and Verseveldt (1942).

Further samples identified as *Anthothela grandiflora* were added to the record by Madsen (1944) from the Ingolf Expedition, who also provided a geographic and depth distribution summary for the species.

After a short definition of the family Anthothelidae and the genus *Anthothela*, which did not differ significantly from others already published, Bayer (1956) re-assigned the Hawaiian species, *Clematissa alba* Nutting, 1908 to *Anthothela.* This move necessitated a new species name, *A. nuttingi,* as Bayer assumed Molander’s (1915, 1929) claim that *Clavularia alba* (=*Rhizoxenia alba*) (Grieg, 1887) belonged in *Anthothela* was correct and therefore had precedence for the combination *Anthothela alba*.

In 1961, Bayer described a new species, *A. tropicalis* from the Gulf of Mexico. It differed from the contemporary concept of *A. grandiflora* by the presence of large, bent prickly spicules in the calyx and the cortex giving the colony a rough, spiky appearance. In the final paragraph of the description, Bayer also compared *A. tropicalis* with “*Anthothela pacifica* (Kükenthal)”, claiming they were a “twin pair” (Bayer 1961). This appears to be a reference to the species described by Kükenthal (1913) as *Clavularia pacifica,* collected from the Californian coastline. Bayer’s passing reference to it as *A. pacifica* suggests the generic re-assignment (from *Clavularia* to *Anthothela*) had been published before Bayer’s comment. However, other than Molander’s (1929) suggestion that this species was not a true *Clavularia* and might be considered a “Scleraxonier (Briareidae?)”, no mention of a re-assignment can be found. It is possible there was no formal re-assignment and Bayer was simply stating accepted wisdom. The combination *C. pacifica* is still in current use (see international databases) and Williams (2000) mentions *C. pacifica* in a comparison with a new genus and species of Clavulariidae.

Another species, *A. parviflora*, collected from waters around South Africa, was added to *Anthothela* by Thomson (1916). This was another significant expansion of the recorded distribution of the genus. This colony also had an arborescent growth form like *A. argentea* and so differs from that of Sars' original description for *A. grandiflora.* Thus, including the two colony forms mentioned by Stiasny (1937) as discussed above, *Anthothela* now had four possible colony forms; a tangled mass of branches with many anastomoses, a flat membranous plate from which robust, upright stems with little or no anastomoses arise, exclusively membranous colonies, and an arborescent growth form with a central trunk.

2.1.3 Encrusting colonies

Over time a number of membranous specimens from deep water, with polyps and sclerites morphologically similar to those described for *Anthothela*, were assigned to many genera including *Clavularia, Anthelia, Gymnosarca, Rhizoxenia, Trachythela* and *Sympodium* (Broch 1912a, 1935; Grieg 1887; Koren & Danielssen 1883; Kükenthal 1906b; Madsen 1944; Saville Kent 1870; Verrill 1922). They typically were described as having warty spindles and clubs arranged *en chevron* into eight converging lines on the polyp head, with similar sclerites in the calyx and the colony surface. There was much discussion over the importance of whether the dorsal part of the polyp could retract (or invaginate) into the calyx and if a "pseudocalyx" was equivalent to a true calyx (Hickson 1894; Kükenthal 1906a; Molander 1915, 1918a, 1918c). The taxonomic disorder and confusion of some parts within the family Clavulariidae was and remains substantial.

In a brave but debatably ineffective attempt at gaining some clarity, Molander (1929) discussed the membranous forms of the "Alcyonarien und Gorgonarien" and suggested the reassignment of many species and questioned the legitimacy of many genera (e.g. *Anthelia, Trachythela* and *Scleranthelia*). As mentioned, he suggested that *Anthelia fallax, Anthelia borealis* (=*Clavularia borealis)* and *Clavularia alba* should be assigned to *Anthothela* but also declared three other *Clavularia* species (*C. pacifica* (Nutting) (sic), *C. eburnea* Kükenthal, 1906 and *C. morsebii* Hickson, 1915) were not valid *Clavularia* species and were perhaps "Scleraxonier (Briareidae?)". As these were only posed as suggestions and were not consolidated with any formal re-assignments or re-descriptions they remain as Molander's opinion. However, the suggestions do function as flags to indicate species with possible erroneous assignations and illustrate the confusion which exists currently.

2.1.4 Existing phylogenetic knowledge of *Anthothela*

In more recent years, efforts to clarify systematic relationships within the octocoral group using molecular phylogenetics have consistently demonstrated that most existing subordinal and many familial groupings are polyphyletic (Berntson 1998; Berntson et al. 2001; Daly et al. 2007; McFadden et al. 2011; McFadden, France, et al. 2006; McFadden et al. 2010; Sánchez, Lasker, et al. 2003). The family Anthothelidae was found to be comprised of "phylogenetically heterogeneous groups of genera"—genera which were found both within and without of a well-supported sub-ordinal clade (McFadden, France, et al. 2006). Although individual colonies identified as *Anthothela* have been included in some higher order phylogenetic studies (Berntson 1998; France & Hoover 2001; McFadden, France, et al. 2006), there has been no molecular phylogenetic analysis that included more than one species of nominal *Anthothela*.

2.1.5 Aims and summary

The definition and morphological characterisation of the genus *Anthothela* has been expanded numerous times, to the point where the genus boundaries are ill-defined and ineffectual. Additionally, the species within the genus are poorly delineated morphologically and there is a lack of any molecular analyses of the species nominally within the genus.

This chapter aims to review and clarify the taxonomic status, definition and scope of the genus *Anthothela* by combining morphological and molecular data. It includes the type specimens of known *Anthothela* species, specimens which have been identified as *Anthothela* historically, plus fresh specimens considered likely to be *Anthothela.* The genus has not been recorded from Australia previously, so recently collected specimens from Australian waters which were assumed to be *Anthothela* were the catalyst for this review. A molecular phylogenetic analysis aims to facilitate a dual approach to the review. Given the existing confusion in the morphological classification of *Anthothela* and evidence that medulla structure and colony form do not necessarily correspond to monophyletic groups (McFadden, France, et al. 2006), it is hoped that the phylogenetic analyses of these specimens will facilitate robust conclusions and greater confidence in taxonomic decisions. The molecular analysis also aims to assist in defining phylogenetically reliable morphological characteristics which correspond to genetic clades.

The results of this review include the confirmation of four existing species and the description of two new species within the genus *Anthothela*. It has necessitated the reassignment of three former species of *Anthothela* to the genus *Victorgorgia* López-González & Briand, 2002 and the addition of two new species to that genus. Finally, the erection of two new genera, *Lateothela* n. gen. and *Williamsius* n. gen.*,* was necessary to accommodate the diversity of species originally thought to be

Anthothela. At a generic level, molecular clades corresponded precisely with morphological groupings; however at a species level some molecular clades corresponded with morphological species but the level of genetic variation found was sometimes too low to enable confident species delineation. A morphological key which distinguishes genera nominally in the subfamily Anthothelinae is included. A key to species within the studied genera was deemed ineffectual given the importance of qualitative sclerite form in distinguishing species and the heavy reliance on illustrations for differentiation. Finally, further effort is made to clarify other taxa which have, at times, been erroneously aligned with *Anthothela* but which do not fit into any of the aforementioned genera.

2.2 Materials and Methods

2.2.1 Samples

Ninety samples were investigated morphologically and were sourced from a variety of research voyages and from many institutions. Type specimens of the seven nominal *Anthothela* species were examined, plus the type specimens of twelve other species which have previously been confused with *Anthothela* or were known to have similar morphological characters to that of *Anthothela*. When possible, museums were visited to facilitate searches of the entire collection of *Anthothela*-like specimens, and when visitation was not possible, museum specimens determined as *Anthothela* were loaned. Unidentified samples from recent research voyages were included if preliminary assessment indicated that they were similar to *Anthothela*. Recently collected specimens were from the seamounts south of Australia and Macquarie Ridge, near Macquarie Island, Norway, the east coast of Canada and the Gulf of Mexico. See 'Material examined' in section 2.3.2 for the collection details of each sample examined.

2.2.2 Terminology and taxonomic characters

Traditionally, the key characteristics used to define *Anthothela* have been medulla structure, polyp distribution, the ability of a polyp to fully retract into a calyx, and the form, location and arrangement of the sclerites. This study has found the form of the sclerites present in the tentacles and pinnules is an under-utilised taxonomic character and this has necessitated redefinition of some sclerite forms and the naming of new sclerite forms. Other characters found to be phylogenetically useful such as boundary canals, boundary space and central medulla canals, are clarified as is polyp and calyx form.

Boundary canals: a ring of longitudinal coelenteric canals separating the medulla from the cortex; canals are adjacent but separate, anastomoses absent or rare (*Anthothela, Lateothela* n. gen., *Williamsius* n. gen.) (Fig. A).

Boundary space: a space encircling the medulla, separating it from the cortex; consists of anastomoses of the boundary canals (*Victorgorgia)* (Fig. B). (The term was first used by Verseveldt (1940) in a discussion on *Anthothela grandiflora* but it is unclear whether he was examining true *Anthothela* specimens or a mixture of genera.)

Calyx (plural calyces): cylindrical, pyramidal or cup-like projections of the coenenchyme into which a polyp can be retracted; calyces cannot be retracted into colony surface (Figs. C; D).

Collaret: a ring of transversely placed sclerites encircling the base of the polyp head, below the points (Figs. C; D).

Cortex: the coenenchymal layer in scleraxonians, surrounding the medulla and containing the polyps of the colony (Figs. A; B).

Medulla: the inner supporting structure of a scleraxonian; contains fused or non-fused sclerites and with or without gorgonin surrounding the sclerites (Figs. A; B).

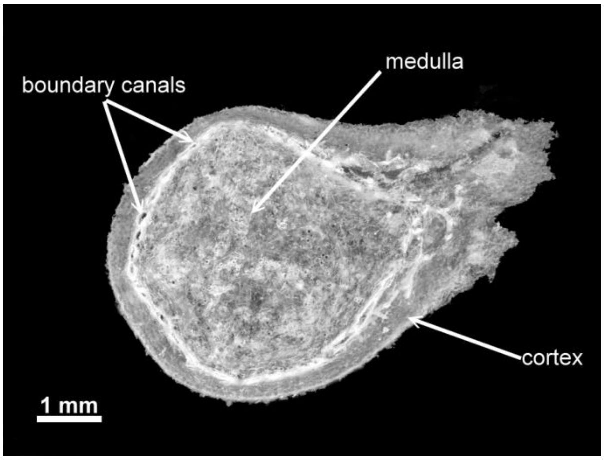


Figure A. Cross-section of the holotype of *Anthothela grandiflora* showing boundary canals, adjacent but separate, and a medulla lacking any obvious central canals.

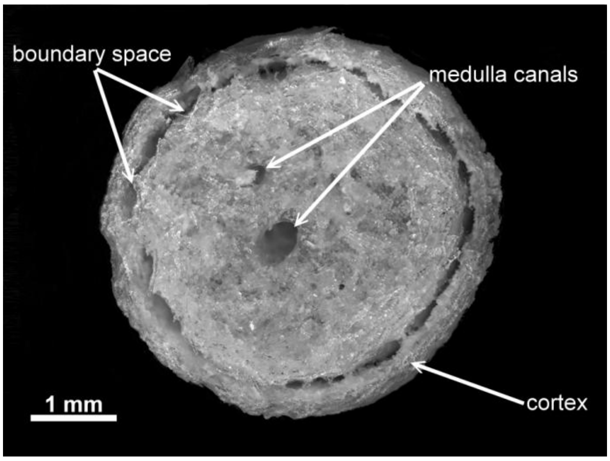


Figure B. Cross-section of the holotype of *Victorgorgia eminens* n. sp. showing extensive boundary canals which frequently anastomose and distinct central canals in the medulla.

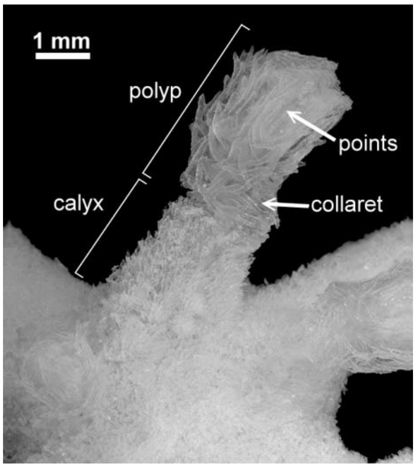


Figure C. Extended polyp of the holotype of *A. aldersladei* n. sp. showing polyp, calyx, points and collaret.

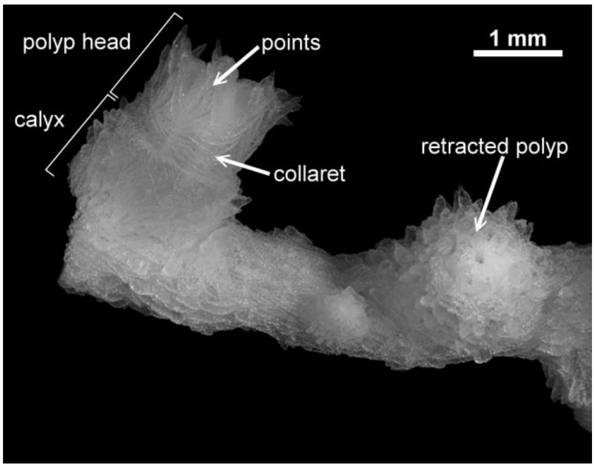


Figure D. Partly extended polyp of *A. quattriniae* n. sp. showing polyp head, calyx, points and collaret and, on right, a fully retracted polyp.

Polyp or anthocodia: all that can extend above the colony surface or calyx in a fully expanded polyp, including polyp head, neck and tentacles; can be retracted into the calyx (Figs. C; D).

Retraction: when the neck of a polyp is invaginated or folded on itself, so the whole polyp can be withdrawn completely or partially below the colony surface or within a calyx (Fig. D).

Sclerite: a calcareous element, irrespective of form, in the polyp, coenenchyme and medulla

Josephinae club: a sclerite with a long, narrow handle and a rounded, often bent, clubbed tip; occurs in tentacle rachis and pinnules; covered in simple tubercules (*Victorgorgia*) or with extensive spikes and thorns (*Lateothela* n. gen.), more dense at the club head (Fig. E).

Spatulate club: a sclerite with a long, narrow proximal handle and a flattened, splayed, distal tip; sparsely covered in simple tubercules; occurs in tentacle rachis and pinnules of *Anthothela* (Fig. E).

Thorn club: a club which has the head developed into thorns and spines, sometimes foliate and covered with tubercles, the handle tending to be longer than the head; a sharp thorn club is one which has the distal tip of the head developed to a sharp point with the head usually at an obtuse angle to the handle (Fig. F). (In Bayer et al. (1983) on Plate 18, Fig. 166 is labelled a “thorn club” but this is inconsistent with other thorn sclerites mentioned and figured (thornscales, thornstars, thornspindles) which all have one or more dominant spires or thorns projecting from the sclerite. Possibly the figure was mislabelled; but regardless, the sclerite should not be considered a thorn club.)

Bulbous thorn club: a thorn club with a pointed, yet bulbous, head that is ornamented with simple to foliate thorns and spines; the handle is covered in complex warts (Fig. F).

Hockeystick spindle: a bent spindle in which the distal end is developed into thorns and spines and the proximal end sometimes has a root; the distal end is longer than the proximal end (Fig. F).

Spiny-spindle: a straight or curved narrow stick-like spindle with large, irregular tubercles and minimal tapering at the ends; as in Bayer et al. (1983), figure 101.

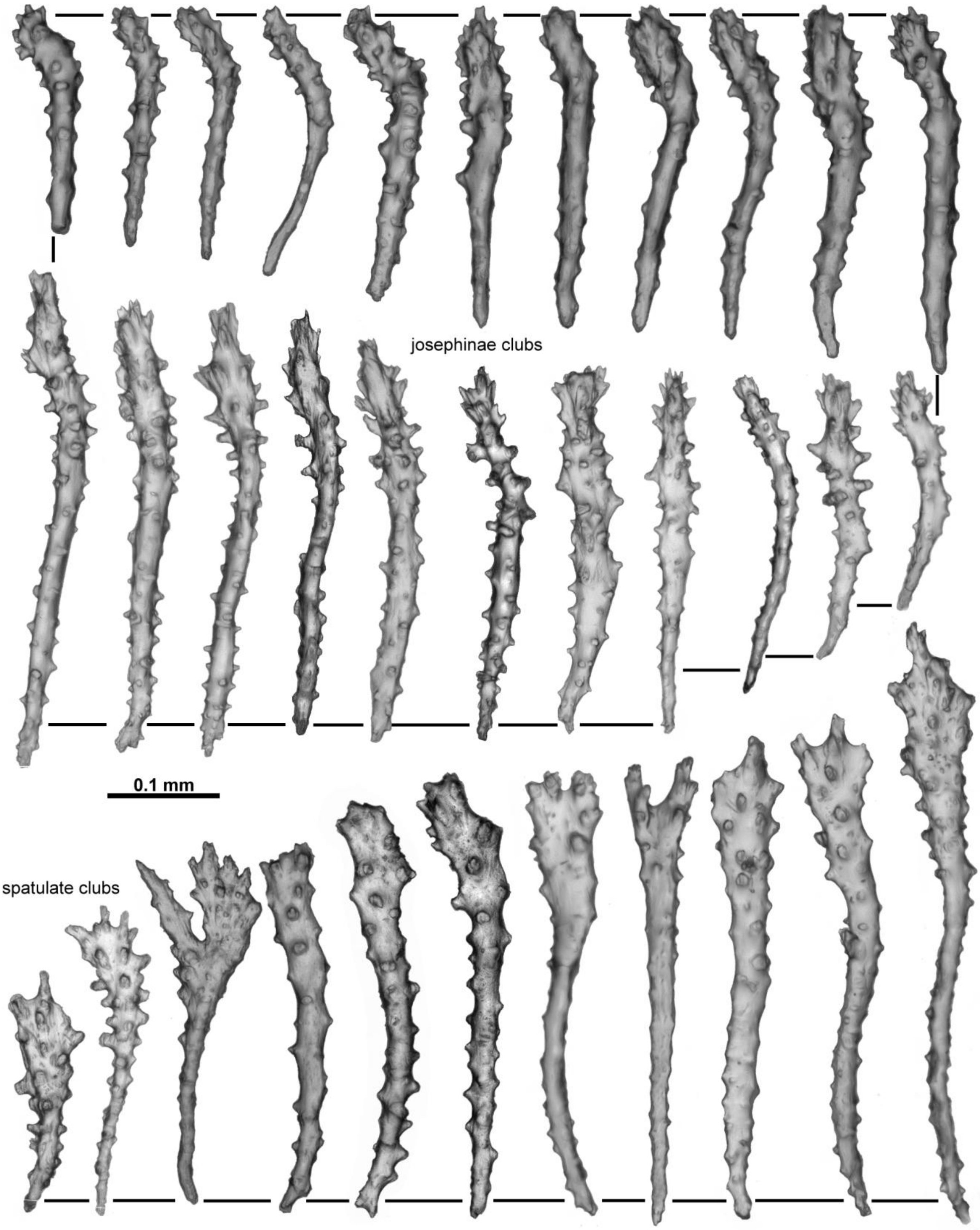


Figure E. Sclerite forms found in the pinnule and tentacle rachis of *Victorgorgia, Lateothela* n. gen. and *Anthothela.*

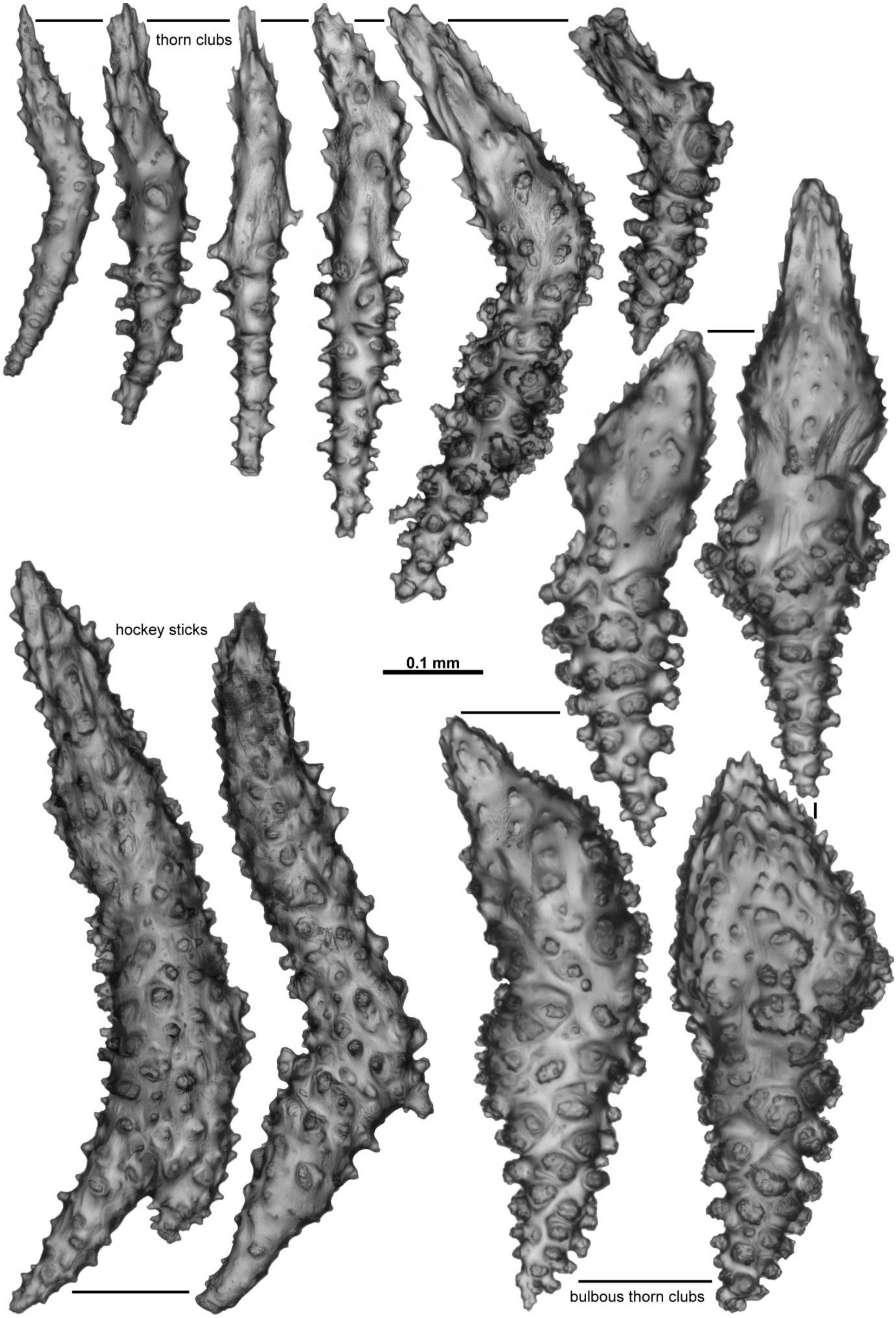


Figure F. Sclerite forms found in the points, calyx and cortex of *Anthothela* and *Victorgorgia* species.

2.2.3 Morphological Methods

Morphological characteristics of colonies were investigated using methods described in Alderslade (1998) and Fabricius and Alderslade (2001). Colony shape, size, branching architecture and the presence/absence of an encrusting portion were noted. Whole colony photographs were taken but varied in method and thus in quality as dictated by the situation. Those colonies examined in international museums were often photographed with constraints on time, facilities and equipment. Some colonies were photographed by the host museum and a small piece only was sent for examination.

Shape and position of polyps and calyces were noted, particularly placement around the branches as traditionally the occurrence (or non-occurrence) on one side of a colony only has been considered of taxonomic importance. Similarly, the ability of the polyp to fully retract into the calyx was recorded. Morphological measurements included total height of colony where possible, degree of branching (primary, secondary etc), diameter of branches, distances between calyces and length and width of calyces and polyps (up to 10 per colony if possible). Measurements were taken using callipers or a graticule under a dissecting microscope to the nearest millimetre. If applicable, details of holdfasts, membranous portions and substrate were also noted.

Sclerites were sampled and isolated from the following zones of the colonies: pinnules and tentacle rachis, points and collaret, polyp neck, pharynx, calyx, cortex and medulla. In each case, a small piece of tissue was dissected out from the surrounding area and dissolved in a drop or two of liquid chlorine (sodium hypochlorite; 125 g/L available chlorine) on a microscope slide. Using a Leica DM1000 compound microscope, the dissolution process was observed and noted where necessary as this aided the process of confirming the positioning of the sclerites.

It quickly became evident that the sclerites on the back of the tentacles were often species-specific and important for taxonomic placement, thus the arrangement of the sclerites in the tentacle rachis and pinnules was photographed. Dissections were performed such that single tentacles could be removed with minimal disturbance to their sclerites. The tentacles would then be soaked overnight or longer in a 2M solution of KOH to clear body tissue, leaving the sclerites clearly visible in situ. The position of the sclerites could then be photographed.

For the purposes of making comparisons and initial identifications based on morphology, sclerites were drawn using a Leica drawing tube. For final descriptions, sclerites were photographed on a Leica DM2000 compound microscope with an attached Leica DFC420 camera. The same camera was used for photographs of polyps, calyces and cortex on a Leica MZ95 dissecting microscope. Photograph stacks were obtained by manually focussing the microscope through the area of interest, and stack-resolving software (Combine Z; Alan Hadley; http://www.hadleyweb.pwp.blueyonder.co.uk/ (accessed 2010)) was used to merge the photographs into a montage. Individual sclerites were then selected and arranged into plates. Photographs were manipulated and improved using image processing software.

Sclerite length was measured on the final photographic plates and additional low resolution photographs if necessary. Where possible, up to 50 sclerites were measured for each region investigated (e.g. tentacles, calyx or surface) for each specimen.

Cross-sections of the branches or stems were necessary to document the placement, size and occurrence of coelenteric canals, around and within the medulla. Photographs of thin cross-sections were sometimes sufficient, but for enhanced clarity slices of axis were soaked in concentrated acetic acid overnight or until the sclerites were dissolved, leaving the tissue structures intact and visible. Montage photographs were then taken of the cleared cross-sections.

2.2.4 Molecular Methods

Of the ninety specimens used for morphological taxonomic review, only samples which had been collected since 2000 were used for molecular analysis because previous studies have shown that coral DNA degrades relatively quickly (Miller et al. 2010). There was an exception of two samples collected in 1997 which were sequenced successfully.

2.2.4.1 Extraction, amplification, purification and sequencing

Total genomic DNA was extracted from a few polyps from each colony using the standard protocol of the Qiagen DNeasy Kit with the following adjustments: all samples were incubated overnight in the lysis buffer, and during the final elution step the AE buffer was warmed to approximately 50°C and the samples were left for 10 minutes before centrifuging, which significantly increased the final concentration of DNA (Helena Baird, pers. comm.). DNA quality was assessed visually on a 1% agarose gel and final concentration determined using a Nanodrop 8000 (ThermoScientific) and, if necessary, the DNA was diluted to a final concentration of 20–30ng/µl.

Two mitochondrial gene regions, igr1–COI and mtMutS (McFadden et al. 2011) were selected for genetic analysis. The two regions combined are currently the most phylogenetically informative mitochondrial gene regions for octocorals and as yet nuclear gene regions have proved difficult to reliably amplify and sequence (Baco & Cairns 2012; McFadden et al. 2011), although recent studies indicate 28S rDNA is potentially useful for phylogenetic analyses in octocorals. (McFadden, Reynolds, & Janes 2014; McFadden & van Ofwegen 2013).

Initially, PCR reactions of 20µl contained 2µl of 10x polymerase buffer (Sigma-Aldrich Co. LLC.), 3.5-5.0 mM $MgCl_2$, 0.2µM of each primer (Table 2.1), 0.2-0.6µg bovine serum albumen, 250µM of each dNTP, 0.4µl of REDTaq DNA polymerase (Sigma Aldrich) and 0.4-2µl of DNA template (with the final amount of DNA template to be between 5 and 10ng). DNA templates were found to be considerably variable in concentration and quality, and were particularly reflective of sample age and preservation. Thus quantity of DNA template used in the PCR reactions had to vary correspondingly and was adjusted across PCR reactions to optimise amplification success. The PCR conditions were as follows: 94°C for 5 min, then 34 cycles of a three-step program (94°C for 30 s, 48°C for 45s (mtMutS) or 54°C for 30s (igr1-CO1), and 72°C for 1 min), with a 10 min final extension at 72°C. Amplification success was confirmed by running PCR products on 1% agarose gels then viewing them under ultraviolet light. PCR products were purified using a QIAquick PCR purification kit (Qiagen) with the only modification to the kit instructions being the final elution in warm (~50°C) distilled water with the sample left for approximately 10 minutes before centrifuging. Samples were sequenced on an ABI3730xl 96-capillary sequencer at AGRF laboratories in Brisbane, Australia. Poor quality reads were excluded from the final analysis.

Samples which did not amplify were re-run with a modified PCR reaction containing 4µl of 5x polymerase buffer (Finnzymes Phire Reaction Buffer which contains 1.5mM $MgCl_2$ at final concentration), 0.5µM of each primer, 200µM of each dNTP, 0.4µl of Taq DNA polymerase (Finnzymes Phire Hot Start II) and 0.5-2µl of DNA template (with the final amount of DNA template to be between 5 and 10ng) in a total volume of 20uL. The PCR conditions were: 98°C for 30s, then 34 cycles of a three step program (98°C for 10s, 48°C (mtMutS) or 54°C (igr1-COI) for 10s and 72°C for 20-30s), with a 2 minute final extension at 72°C.

In some cases, the DNA proved too degraded to amplify across the entire length of the target gene region. Consequently, internal primers were designed based on entire sequences already obtained from less degraded samples. Primers were designed using the web-based software Primer3 v1.1.4 (http://frodo.wi.mit.edu/primer3/) and were situated in conserved regions approximately in the middle of the two mitochondrial gene regions (Table 2.1). These were used in conjunction with those primers from McFadden et al. (2011) such that two short halves of each gene region could be assembled into a complete longer sequence. The internal primers were only used with the second PCR protocol outlined above (Finnzymes Phire Hot Start II Taq).

Table 2.1. Primers used to amplify two mitochondrial gene regions (igr1–COI and mtMutS) including published external primers and newly designed internal primers. (adapted from McFadden et al. 2011)

Primer		Sequence 5'→3'	Fragment Size	T_m°	Reference
COII(5')-igr1-COI(5'):					
1.1kB					
1)	COII8068F forward	CCATAACAGGACTAGCAGCATC	~1000 (1&4) ~ 600 (1&2)	62.5	McFadden et al. 2011
2)	PRANCOIR reverse	CCTGTACCTGCCCCTTGTT		63.8	This study **(igr1–COIA)**
3)	PRANCOIF reverse	GGATTCGGAAATTGGTTTGT	~ 530 (3&4)	62.4	This study **(igr1–COIB)**
4)	COIOCTR reverse	ATCATAGCATAGACCATACC			McFadden et al. 2011
mtMutS(5'):					
~760 nt					
5)	ND42475F forward	TAGTTTTACTGGCCTCTAC	~990 (5&9) ~ 620(5&7)	50.9	McFadden et al. 2011
6)	ND42599F forward	GCCATTATGGTTAACTATTAC	~870 (6&9) ~490 (6&7)	52.1	McFadden et al. 2011
7)	ANTHMSH1F Reverse	TCCGAACAGTCCTCTAAATTACAA			This study **(mtMutSA)**
8)	ANTHMSH1F forward	GCTTCAAATGGGGTTTCCA	~490 (8&9)	64.3	This study **(mtMutSB)**
9)	MUT3458R Reverse	TSGAGCAAAAGCCACTCC		61.6	McFadden et al. 2011

Sequences were assembled and edited using *MEGA* version 5 (Tamura et al. 2011). When available, consensus sequences were constructed using forward and reverse primer sequences from the same PCR product. Where possible, short sequences generated by the internal primers were concatenated into a single long sequence for each gene region. After conducting BLAST searches in GenBank to confirm the validity of the sequences, the data were aligned in the software package MEGA5 using the alignment algorithm 'MUSCLE' (Edgar 2004) set with default parameters and then adjusted by eye if necessary.

A comparison of the number of variable nucleotide positions, parsimony informative sites and genetic distance from each gene region individually and with the two gene regions concatenated was conducted in MEGA5. For some of the more degraded specimens, only half of a gene region was successfully sequenced so rather than trimming all the sequences to those very short sequences, all sequences were extended to the length of the longest sequence with question marks denoting unknown nucleotides, thereby maximising the number of nucleotide positions in the analysis without significantly affecting accuracy (Wiens & Morrill 2011). Genetic distance as uncorrected pairwise ‘p-distances’ between groups was obtained from MEGA5 to allow comparisons with published sequence variability and genetic distances among and between octocoral species and genera. A character-based analysis (or a comparison of single nucleotide polymorphisms) between taxa was also employed as an additional species delineation tool. This approach has been considered useful when genetic distances and sequence variability are low (Baco & Cairns 2012).

2.2.4.2 Outgroups and additional sequences

In an initial analysis the sequences generated in this study plus a few additional sequences from closely related species were used to generate a phylogenetic tree. Sequences from *Titanideum frauenfeldii* (Kölliker, 1865) and *Homophyton verrucosum* (Möbius, 1861), both in the family Anthothelidae but in a different subfamily (Spongiodermatinae) to *Anthothela* (Anthothelinae), were also included as they are sufficiently divergent from the genera in this study to effectively root the trees and form an outgroup.

Sequences from GenBank of many additional species and genera (Appendix 2) were included in a second phylogenetic analysis to help elucidate the relationships among the *Anthothela* samples studied here and to give context to the phylogenetic position of *Victorgorgia* and the new genus *Lateothela*. In particular, to illustrate the interlacing of the two genera *Anthothela* and *Alcyonium* Linnaeus, 1758, sequences (of both mtMutS and igr1–COI) of nominal *Alcyonium* species available in GenBank (Appendix 2) and additional sequences from Catherine McFadden (Harvey Mudd College, USA) were added (Table 2). Concatenated sequences from two *Alcyonium* species from each of four clades found by McFadden et al. (2011; 2001) were included. Additionally, sequences identified on GenBank as *Anthothela nuttingi* (=*Clematissa alba*) and *Trachythela rudis* (=*Clavularia rudis*) Verrill, 1922 were included in the phylogenetic trees. In most cases voucher specimen numbers were available in GenBank or specified in McFadden & Ofwegen (2012c) and thus, for each voucher specimen, the two gene regions could be confidently concatenated (Appendix 2). When voucher specimen numbers were not available or could not be traced in publications, the two sequences to be concatenated for those species were selected based on at least one concurrent author.

Sequences of both gene regions from four *L. anitorkilda* n. gen., n. sp. specimens and one *A. quattriniae* n. sp. specimen from Andrea Quattrini (Temple University, USA) were included as were sequences from three specimens of *Trachythela rudis* (Table 2.2). All are specimens from the Gulf of Mexico and all have been included in the morphological analysis as well.

For some relevant specimens, only one of the two gene regions was available. In these situations the sequences were added to analyses conducted on single gene regions only. Specifically a sequence identified as *Anthothela* sp (GenBank DQ297415), a sequence identified as *A. nuttingi* (S. France pers. comm.), and a sequence which was thought to be from *A. grandiflora* (but grouped with *Lateothela anitorkilda* n. gen., n. sp. specimens) were added to the mtMutS analysis (Table 2.2).

Table 2.2. Details of additional sequences sourced directly from researchers.

Gene Region	Species	Voucher specimen	Researcher
both	*Lateothela anitorkilda*	USNM 1139021	Quattrini, A.
both	*Lateothela anitorkilda*	USNM 1207952	Quattrini, A.
both	*Lateothela anitorkilda*	USNM 1207953	Quattrini, A.
both	*Lateothela anitorkilda*	TMAG K4272	Quattrini, A.
both	*Anthothela quattriniae*	USNM 1207951	Quattrini, A.
both	*Trachythela rudis* (=*Clavularia rudis)*	LII-10-679	Quattrini, A.
both	*Trachythela rudis* (=*Clavularia rudis)*	LII-09-185	Quattrini, A.
both	*Trachythela rudis* (=*Clavularia rudis)*	LII-10-629	Quattrini, A.
mtMutS	*Victorgorgia alba* (=*Anthothela nuttingi*)	USNM 98795	France, S.C.
mtMutS	*Anthothela grandiflora*?	BLT2011	France, S.C.
mtMutS	*Alcyonium grandiflorum*	RMNH Coel. 33874	McFadden, C.
mtMutS	*Alcyonium rubrum*	RMNH Coel. 33879	McFadden, C.

2.2.4.3 Phylogenetic Analyses

Phylogenetic analyses were conducted on two distinct groupings—an initial analysis only on specimens sequenced for this study which matched the morphological genera within the review and then a second extended analysis which included additional sequences (from this study, from GenBank and directly from other researchers).

The most appropriate model for sequence evolution and phylogenetic reconstruction was assessed for each gene region using the software package jModelTest Version 2.1.4 (Darriba, Taboada, Doallo,

& Posada 2011; Guindon & Gascuel 2003) based on scores of AIC (Akaike Information Criterion). The two gene regions were assessed separately for appropriate models as they are potentially evolving separately. For the first analysis with fewer sequences, the model HKY +G was found to be the most applicable model for each of the gene regions and thus could be used for the concatenated analysis without partitioning. For the second analysis with a wider scope, models were re-assessed for each gene region and the most appropriate was found to be GTR+G +I for mtMutS only, and TVM+G +I for igr1—COI. As this exact model is not available in MrBayes, GTR+G +I was used for the concatenated gene regions.

Maximum likelihood (ML), conducted in MEGA5 and Bayesian analysis, conducted in the software package MrBayes v.3.1.2 (Huelsenbeck & Ronquist 2001), were used to construct phylogenetic trees for cladistic assessment of genus and species groupings. In MrBayes, priors were adjusted accordingly to implement the appropriate models, including using a partitioned model for the larger analysis where the recommended models differed between the two gene regions. The Markov Chain Monte Carlo (MCMC) analysis was run with 2 runs, 4 chains, sample frequency of 100 and a burn-in of 25%. Analyses were run for the number of generations required to achieve an average standard deviation of split frequencies of <0.004 between the two runs. Phylogenetic trees were viewed and prepared for publication in FigTree v1.3.1 (Rambaut 2006-2009).

2.3 Results

2.3.1 Summary of taxonomic decisions

The specimens examined initially consisted of type material of all the nominal species of *Anthothela* and numerous specimens either identified as *Anthothela* or that appeared to conform to the current understanding of the genus. This suite of specimens was found to be a mixture of four genera; *Anthothela, Victorgorgia* (which necessitated an examination of the holotype of the type species, *V. josephinae)*, and two new genera *Lateothela* n. gen. and *Williamsius* n. gen. based on both morphological and molecular data. A major conclusion was that the form of the sclerites in the tentacle rachis and pinnules, combined with medulla structure and colony form, is indicative of a particular genus, and molecular support was found to be definitive and unambiguous at the genus level.

A total of six species are now recognised within the genus *Anthothela*. Characteristics for species delineation include variation in sclerites and geographic distribution but molecular differences at a species level were found to be slight. The type species *A. grandiflora* (Sars, 1856) plus *A. pacifica* (Kükenthal, 1913) and *A. tropicalis* Bayer, 1961 are redescribed and retained as valid species, *Spongioderma (?) vickersi* Benham, 1928 is re-assigned to *Anthothela* (Table 2.3) and two new species are described, *A. aldersladei*. and *A. quattriniae*.

Within the genus *Victorgorgia,* six species are now recognised. The type species *V. josephinae* López-González & Briand, 2002 is reviewed with minor additions to the description; three species, *Anthothela argentea* Studer, 1894*, A. macrocalyx* Nutting, 1911 and *Clematissa alba* Nutting, 1908 (= *A. nuttingi* Bayer 1956) are re-assigned to *Victorgorgia* (Table 2.3); and two new species are described, *V. eminens* and *V. nyahae*.

Lateothela anitorkilda n. gen.*,* n. sp. is described to accommodate a suite of specimens, some of which have been assumed to be *A. grandiflora* for approximately 150 years, and the species *Anthothela parviflora* Thomson, 1916 is re-assigned to a new genus *Williamsius* (Table 2.3).

Molecular results in general supported the morphological conclusions, particularly at the generic level (Figs. 2.140; 2.141). *Anthothela* and *Lateothela* n. gen. were found to be phylogenetically closely related to some clades of nominal *Alcyonium* species, while *Victorgorgia* was found to be genetically distant from all these genera and more closely related to other membranous species. At the species level, genetic differentiation was often slight and unresolved and hampered by small specimen numbers, in which case morphological and geographical differences were employed for species delineation.

Some species which have been confused with *Anthothela* historically, such as *Anthelia fallax, Clavularia borealis* (=*Anthelia borealis*)*, Clavularia griegii* Madsen, 1944 and *Trachythela rudis* (=*Clavularia rudis*), were found not to be con-generic and relevant characteristics and comparisons are discussed.

Table 2.3. Original placements, subsequent reassignments and current or new designations of recognised *Anthothela* species.

Original designation	Author	Assigned to	Assigned by	Current or new designation
Briareum grandiflorum	Sars, 1856	*Anthothela grandiflora*	Verrill, 1879a	*Anthothela grandiflora* (Sars, 1856)
Anthothela argentea	Studer, 1894			*Victorgorgia argentea* (Studer, 1894)
Clematissa alba	Nutting, 1908	*Muriceides alba*	Kükenthal, 1924	
		↓		
		Anthothela nuttingi	Bayer, 1956	*Victorgorgia alba* (Nutting, 1908)
Suberia macrocalyx	Nutting, 1911	*Semperina macrocalyx*	Kükenthal, 1916	
		↓		
		Anthothela macrocalyx	Verseveldt, 1942	*Victorgorgia macrocalyx* (Nutting, 1911)
Clavularia pacifica	Kükenthal, 1913	*Anthothela pacifica*	? referred to by Bayer 1961	*Anthothela pacifica* (Kükenthal, 1913)
Anthothela parviflora	Thomson, 1916			*Williamsius* n. gen. *parviflora* (Thomson, 1916)
Spongioderma (?) vickersi	Benham, 1928			*Anthothela vickersi* (Benham, 1928)
Anthothela tropicalis	Bayer, 1961			*Anthothela tropicalis* Bayer, 1961

2.3.2 Systematic account

ANTHOTHELIDAE Broch, 1916

Anthothelidae Broch, 1916: 14

Diagnosis:

Monomorphic scleraxonians with a central medulla, which may contain longitudinal coelenteric canals, formed of tightly packed but not fused sclerites, separated from the cortex by a boundary of longitudinal canals which may anastomose to form a boundary space; polyps retractile into calyces; sclerites comprised of tuberculate rods, spiny-spindles (often clavate or bent), clubs, radiates and capstans.

Remarks:

The family Anthothelidae was originally created to incorporate scleraxonian specimens with a ring of boundary canals separating the cortex from the medulla. This family grouping is now in doubt with evidence that the family is polyphyletic (McFadden et al. 2010).

Anthothela Verrill, 1879

Anthothela Verrill, 1879b: 199; 1883: 40; Studer 1887: 28; Wright & Studer 1889: xxxiii; (part) Broch 1912b: 4; 1916: 12–14; ?Kükenthal 1916: 174; (part) 1919: 20–31, 43, 103–107, 685, 696, 725–728, 796, 818–826, 874–878, Tafel LVI Karte I., Tafel LXXV; (part) Verrill 1922: 18; (part) Kükenthal 1924: 9, 14; Aurivillius 1931: 10; ?Deichmann 1936: 75, 78; (part) Stiasny 1937: 19; Carlgren 1945: 33; Bayer 1956a: 86; Bayer 1956b: F194; Bayer 1961: 67; Mikosz Arantes & de Medeiros 2006: 12.

?Gymnosarca Kent, 1870 but see Stiasny, 1937: 19.

Type species: *Briareum grandiflorum* Sars, 1856, by designation

Diagnosis:

Monomorphic scleraxonians which form both membranous and branched colonies. Branched colonies are tangled with no central or main stem; anastomoses common; cortex separated from medulla by a ring of intact coelenteric canals; coelenteric canals almost always absent from central medulla (occasionally present as only a thinning in the density of sclerites); calyces distinct, cylindrical to conical, spread irregularly throughout colonies with little free space between, tending to crowd together at branch tips; polyps often exsert but may be partly or fully invaginated into calyces; medulla sclerites are straight, simple spiny-spindles with light to moderate tuberculation; all other sclerites are spiny-spindles, clubs and hockeystick spindles, many clubs are bent with thorny tips; arranged as collaret and points on polyp head and longitudinally along the aboral side of the tentacle rachis; pinnules are crowded with longitudinally arranged, narrow spatulate clubs; the pharynx has small tuberculate rods. Membranous colonies are as above but lack a medulla.

Remarks:

Specimens of *Anthothela* have historically been understood to be a relatively common occurrence amongst deep-water samples from the Northern Atlantic. In reality, the understanding of *Anthothela* had been so modified and expanded as to ultimately incorporate specimens which were actually from other genera. The removal of these specimens means the diagnosis of *Anthothela* has now been refined and tightened. The world-wide distribution of the genus remains with confirmed records from the north and south Atlantic Ocean, southern Indian Ocean, north and south Pacific Ocean and on the northern boundary of the Southern Ocean. All occurrences are restricted to cold waters with most specimens collected deeper than 100m down to over 1800m in depth.

***Anthothela grandiflora* (Sars, 1856)**

(Figs. 2.1–2.12)

Briareum grandiflorum Sars, 1856: 63–65, Pl. X Figs. 10–12; 1857: 238; Storm 1879: 123; 1892: XXVII.

Anthothela insignis Verrill, 1879a: 15.

Anthothela grandiflora Verrill 1879a: 32; 1879b: 199; 1883: 40, Pl. IV Figs. 6, 6a; 1885: 535; Storm 1896: XXI; Storm 1901: 11; Whiteaves 1901: 32; (part) Broch 1912b: 5–9, Figs. 1–3; (?part) Molander 1918: 6–8, Fig. 1; ?Kükenthal 1919: 17, 19, 26, 43–44, 672, 681–685, 730, 788, 796, Figs. 17, 315; (part) Verrill 1922: 18–19, Fig. 2, Pl. VI Figs. 1–4; ?Kükenthal 1924: 14–16, Figs. 13–14; (part) Thomson 1927: 16–18, Pl. I Fig. 20, Pl. III Fig. 34, Pl. IV Figs. 6, 16, Pl. V Fig. 28; Molander 1929: 35–37; Thomson 1929: 4; Aurivillius 1931: 10; ?Deichmann 1936: 75, 78–79; (part) Stiasny 1937: 20–23, Figs. F^1, F^2, Pl. I Figs. 6, 7; ?Verseveldt 1940: 37–47, Figs. 13–15; (part) Madsen 1944: 32–33, Fig. 32; Carlgren 1945: 33–34, Fig. 8; Bayer 1956b: F194, Fig. 140,3; Bayer 1961: 67–68; Tixier-Durivault & d'Hondt 1974: 1393; Grasshoff 1981: 745, Karte 1, 942; Carpine & Grasshoff 1985: 11–12; Bayer & Cairns 2004: Pl. 64 Fig. 8, 8b; Watling & Auster 2005: 292; Mikosz Arantes & de Medeiros 2006: 11–17, Figs. 1–4.

?Gymnosarca bathybius Saville-Kent 1870: 397, Pl. 21 Figs. 1–4 but see Stiasny, 1937: 19.

NOT: *Anthothela grandiflora* Möbius 1873: 260 [→*Eunephthya?*] see Madsen 1944

Doubtful: *Anthothela grandiflora* Storm 1879: 144, 337 [→*Anthelia fallax* Broch, 1912]

NOT: *Anthothela grandiflora* Grieg 1890: 11 [→ *Paramuricea* sp]

Doubtful: *Anthothela grandiflora* Grieg 1894: 3, Pl. I Figs. 1–2 [→*Lateothela anitorkilda* n.gen., n.sp.]

Material examined:

Holotype: NHM, UIOslo B1365, Öxford, Finmark, northern Norway, depth 365 m, no date recorded; **ZMUC no number**, same data as holotype and noted as a "co-type".

Other material: **NTNU-VM 63139**, Agdeneståa, Trondheimsfjord, Norway, 63.646°N, 9.752°E, depth 100–250 m, Torkild Bakken, 21st June2001; **NTNU-VM 63141**, Rødberg, Trondheimsfjord, Norway, 63.468°N, 9.999°E, depth 200–300 m, Torkild Bakken, 5th December 2006; **NTNU-VM 40341 (part)**, Dyrviknes 27, Trondheimsfjord, Norway, 63.603°N, 9.757°E, depth 120 m, 18th May 1965; **NTNU-VM 67148 & 67149**, Brettingen**,** Trondheimsfjord, Norway, RV *Gunnerus,* stn. 2011022, 63.659°N, 9.798°E, depth 200–100 m, Torkild Bakken, 14th June 2011; **NTNU-VM 40338 & 40339**, unknown locality, determined by Broch 1912; **ZMUB 17759 (part)**, Skarnsundet, Trondheimsfjord, Norway, August 1899; **ZMUB 12187**, Molde, Julneset, Midfjord, Norway, RV *G.O.Sars*, stn. 101, depth 275 m; **ZMUB 60328**, Langenuen, Klinkholmen, Tysnes, Norway, August 1894; **ZMUB 455**, Haakonsund, Norway, determined by Danielessen & Koren; **NHM,UIOslo B1366**, Selsövik, Norway, depth 182 m; **ZMUC-ANT-000470,** Brettingsnes, Trondhjemsfjord, Norway, depth 150 m, 21st September 1934; **ZMUC-ANT-000469,** Rødberg, Trondhjemsfjord, Norway, depth 150–300 m, 17th July 1911; **ZMB 5527 (part),** Rødberg, Trondheimsfjord, Norway, depth 300–350 m, 1913; **MCZ 51047,** Banquereau Bank, off Nova Scotia, Canada, U. S. Fish Commission no. 5705, Gloucester Fisheries Lot 418, 44.217°N, 58.033°W, depth 320 m, 1973; **MCZ 51048,** unknown locality; **MCZ 50734,** Browns Bank, east coast of Canada, schooner *Chester B. Lawrence*, 42.517°N, 64.333°W, depth 300 f (feet or fathoms), Capt. Wm. H. Greenleaf; **MOVI 20919,** east coast of Rio Grande do Sul, Brazil, 34.324°S, 51.572°W, depth 822 m, 5th March 2002; **unregistered specimen,** NEREIDA 0610, zone NAFO, tow DR72, 46.0239°N, 46.686°W, depth 710 m, collected by Tina Molodtsova thanks to Mar Sacau and Javier Murillo Perez (IEO, Vigo, Spain) and sampling program NEREIDA, 28th June 2010.

Description:

Colony form:

The holotype is made up of many fragments of a tangled colony which once was described as "die Grösse eines Menschenkopfes" (translated as the size of a human head) (Broch 1912b) (Fig. 2.1A). There is no central trunk or evidence of main branches and there is no consistent arrangement of branching. In Sars' original description, he made it clear ("D'ailleurs il n'y a aucune différence entre les tiges et les branches: elles ont la même apparence, la même forme, la même grosseur“) that there is no difference between stems or branches: they have the same appearance, same form and same size. Many of the fragments are small pieces of narrow branches which are often twisted and tangled so it is impossible to reconstruct the colony into the original shape. There are also multiple anastomoses and bifurcations throughout the colony fragments (Fig. 2.1B). Examples of membranous portions of the colony are evident including the holdfast which is encrusting a piece of coral rubble. Several branches emanate from the membranous parts of the colony with no discernable change in the colony surface. Most branches are of a relatively uniform diameter (approximately 2.2–3.4 mm), although there are some outside this range (1.3–4.2 mm), and they are basically circular in cross-section, although calyces and bifurcation points tend to cause some distortion.

Calyces occur with no apparent order along and all around the branches throughout the colony leaving little free space. The greatest distance between calyces is approximately 12 mm although they are more commonly closer together. Tight bunches of calyces occur on the branch tips where there is very little or no space between them (Fig. 2.2A). Isolated calyces are also evident on the membranous parts of the colony.

The colony is in good condition, albeit in many fragments, with many polyps still attached and, in general, the cortex is complete.

Colour:

In the original description no mention was made regarding the live colour, although Sars did comment that the medulla is a darker colour than the cortex. The holotype is now light brown to cream in alcohol. Other specimens recently collected are creamy pink (see below).

Polyps and calyces:

Calyces are tall, flat-topped, robust tubes which protrude basically at right angles from the branches (Fig. 2.2B). They are usually between 2.2–3.2 mm high although there are some larger ones up to 4.5 mm, and polyps extend 1.4–2.6 mm above the lip of the calyx and are approximately 2–3mm wide. Calyces and polyps are usually taller than they are wide. Sars considered the relatively large size of the calyces and polyp as a distinguishing factor, mentioning that the height of the “cellules polypifères” is generally twice the diameter of the branches. The calyces do not have obvious longitudinal ridges but can bulge slightly where the base of the tentacles meets the calyx lip. Most of the polyps are partly retracted such that the base of the polyp head rests on the lip of the calyx and the polyp neck is not visible (Fig. 2.2B) but there are some examples where polyps are fully retracted into their calyx (Fig. 2.2Aa) despite Sars stating that he did not observe any fully-retracted polyps. Occasionally fully exsert polyps occur, with the polyp neck visible—a polyp and calyx combined then being up to 6.5 mm high. All polyp heads are well protected by crowded sclerites arranged as points and an indistinct collaret and the visible polyp necks are also covered in sclerites. The tentacles fold into the polyp mouth so the polyp heads are rounded mounds with eight distinct furrows producing a starred appearance (Fig. 2.2B). There are approximately 12 pinnules along each side of the tentacles with a fan of pinnules around the tip.

Medulla:

The central medulla is made up of tightly packed, longitudinally and obliquely placed sclerites, surrounded by a thin cortex which is separated from the medulla by a ring of longitudinal canals (Fig. 2.2C). The canals run parallel and close together throughout the colony and remain identifiable as individual canals. They do not extensively anastomose or form a boundary space as such but do provide a clear separation of the medulla from the cortex. In the thickest branches, presumably older and from closer to the base of the colony, there may be some patches where the density of medulla sclerites lessens. These patches appear as indistinct canals in the central medulla (Fig. 2.2D) and are easily deformed or obscured by sclerites during the making of a cross-section. In thinner branches, presumably younger and farther from the base of the colony, the ill-defined canals in the centre of the medulla are only occasionally visible in cross-section.

For polyps along the branches, body cavities truncate abruptly forming a flat base where they abut the medulla, while polyps which are clumped at the branch tips have a body cavity which extends somewhat deeper within the branch eventually finishing at the start of the medulla proper.

Sclerites:

Polyps, calyces and the cortex are all covered in crowded sclerites. On the polyp head transversely arranged sclerites form an indistinct collaret approximately 8 sclerites deep, while above they are arranged *en chevron* grading to longitudinal in the points (Fig. 2.2B). These sclerites are mostly straight or slightly curved spiny-spindles with simple tubercles (Fig. 2.3). Sizes can range from 0.4–1.3 mm but most are between 0.45–0.85 mm. Some sclerites have the distal tip with mildly more developed tubercles or spines (Fig. 2.3a). Very occasionally, sclerites can have complex warts. Below the collaret, similar sclerites are arranged obliquely on the polyp neck, sparser than on the polyp head, presumably to allow the polyp to invaginate at the neck area.

Along the aboral side of the tentacle, sclerites are arranged longitudinally and are all mostly similar to the sclerites from the points although shorter (Fig. 2.4A). They are straight or slightly curved tuberculate spiny-spindles with complex warts occurring occasionally and processes slightly more developed on one end (Fig. 2.4B). Sclerites grade in size from longest (0.5 mm) at the proximal end of the tentacle to shortest (0.25 mm) at the distal end.

Long, thin, spatulate clubs extend longitudinally most of the way down the pinnules (Fig. 2.5A). These sclerites are crowded, with the spatulate tip in the distal end of the pinnules, and are easily broken during dissection. The spatulate clubs have long narrow handles and flattened, occasionally forked tips and are usually straight but can be curved or with bent tips (Fig. 2.5Ba). There are also short rods with sparse tubercules, narrow spiny-spindles with no flattened tips and very small flanged spindles in the pinnules (Fig. 2.5Bb). The size of the spatulate clubs ranges from 0.34–0.5 mm while the smaller rods and spindles are approximately 0.08–0.21 mm long.

Small rods (0.08–0.24 mm long) with cone-like prominences and sparse warts occur in the pharynx (Fig. 2.6A). These sclerites are arranged in ill-defined lines in the pharynx corresponding to the mesenterial insertions and are not crowded (Fig. 2.6B).

The sclerites of the calyx are arranged in a dense layer, longitudinally to obliquely in the wall. They are short, straight or slightly curved spiny-spindles mostly with simple tubercules (Fig. 2.7). Occasionally more complex warts occur and some sclerites have a clavate tip with slightly flared or foliose spines (Fig. 2.7a) but they do not form true thorn clubs. The sclerites have a small size range only varying from approximately 0.23–0.45 mm long.

The sclerites from the cortex are similar to those in the calyces—small, straight tuberculate spiny-spindles of a fairly uniform shape and size (Fig. 2.8). Most of the sclerites are between 0.16 and 0.38 mm in length but slightly longer sclerites also occur. Occasionally, sclerites with more complex warts occur but more commonly the tubercles are simple and relatively sparse. Some sclerites can have one marginally more complex tip making them slightly clavate (Fig. 2.8a).

The medulla is composed of tightly packed sclerites, mainly spiny-spindles with simple to complex tubercles (Fig. 2.9). There are examples of fusion, branching and forking in some sclerites resulting in quite complex forms. The length of the sclerites can vary considerably (0.2–0.9 mm) and the longest sclerites are probably under-represented as it is difficult to sample them without breakage.

All sclerites are transparent and colourless under transmitted light.

Variability:

Variability of sclerite development within this species appears to be quite substantial. The holotype is from the northern tip of Norway, at the extreme northern point of the distribution of the specimens examined (unfortunately no specimens which are geographically close to the holotype were available), and it is a specimen with a very consistent form of sclerites (spiny-spindles with simple tubercles) from the aboral side of the tentacles, points, collaret, calyx and the cortex. Yet other specimens have considerable variation in the complexity and shape of the sclerites. One specimen, NTNU-VM 67149, from Trondheimsfjord, Norway, has sclerites from the calyx which are more often club-shaped with very complex warts and spines in addition to the spiny-spindles with simple tubercules like the holotype (Fig. 2.10A). Such complex sclerites in the calyx are common in other specimens investigated, particularly in specimens from the Trondheimsfjord, yet the colony and polyp form and the other sclerites are similar to those in the holotype. Photographs of two specimens from Trondheimsfjord taken soon after collection (NTNU-VM 67149 and NTNU-VM 67148) demonstrate the live colour to be creamy pink (Fig. 2.10B, C).

In addition, there are many specimens with more complex and larger sclerites from the tentacles, points and surface than those observed in the holotype. In particular, despite much similarity with the holotype in other areas, the sclerites from the tentacles of ZMUC-ANT-000470 and NTNU-VM 40338 have more developed processes on the distal tips (Fig. 2.11A, B). At this stage, it is assumed they are more complex versions of those in the back of the tentacles of the holotype, although further collections may allow a definitive delimitation within these degrees of complexity.

Similarly, the colony surface of sample NTNU-VM 63139, along with small spiny-spindles like those of the holotype, has numerous short, straight, club-shaped spindles with smooth areas as well as more developed spines and warts (Fig. 2.12). These surface sclerites were recorded in lesser amounts in other specimens as well, but not the holotype.

Distribution:

Confirmed records are from the north eastern Atlantic Ocean in deep coastal waters and fjords of Norway and Iceland; north western Atlantic Ocean, in deep waters off the coast of Canada and USA; the Gulf of Biscay, off the west coast of France and the south western Atlantic Ocean off the coast of southern Brazil.

Unconfirmed records are from deep waters in the central Atlantic Ocean; off the coast of Florida, USA and the Gulf of Mexico; from off the coast of Portugal; Azores Islands and the Cape Verde Islands.

Depth:

Confirmed specimens 100–960 metres; most commonly between 100–500 metres.

The shallowest depth recorded in the literature or against samples determined as *A. grandiflora* is 12 m in Andros Island in the Bahamas (USNM 57344). This specimen was not investigated here but given that *A. grandiflora* is known as a deep water or cold water species it seems highly unlikely that this is a specimen of this species. Specimen USNM 30272 was recorded in only 44 metres of water at Jefferies Ledge, 6 miles off the east coast of northern USA. Again, this specimen was not investigated here but given the depths recorded for confirmed specimens it seems unlikely to be a specimen of this species.

Remarks:

There has been much confusion over many years between *A. grandiflora* and material that has herein been assigned to *Lateothela anitorkilda* n. gen., n. sp. In every collection examined which contained specimens of *A. grandiflora*, *L. anitorkilda* n. gen., n. sp. was also found, almost always erroneously determined as *A. grandiflora.* In Broch's (1912b) extensive re-description of *A. grandiflora* it now seems clear that he included more than one specimen in his description and at least one of these was likely to have been a specimen of *L. anitorkilda* n. gen., n. sp. The figure of the small, warty rodlets from the calyces and cortex (Broch 1912 Fig. 2a, b), which are common in *L. anitorkilda* n. gen., n. sp. but do not occur in any significant number in *A. grandiflora,* perpetuated the confusion between the two genera. One of the chief morphological differences between these two species is the preponderance of these rodlets in the calyces and cortex of *L. anitorkilda* n. gen., n. sp. (mixed with tuberculate spiny-spindles) compared with their rarity in *A. grandiflora.*

Other differences between the two species are colony form and differences in the pinnule and tentacle sclerites. Much of the subsequent literature perpetuated Broch's (1912b) incorrect description thus some later determinations and descriptions of specimens are incorrect or cannot be confirmed (Madsen 1944; Stiasny 1937; Verrill 1922; Verseveldt 1940) and many specimens remain incorrectly identified. For example, Verrill (1922) when describing *A. grandiflora* stated the figures are "from the type described in 1869", however Plate VI Fig. 1 particularly, and his description of the appearance of the calyces appears to depict *L. anitorkilda* n. gen., n. sp. with the small warty rodlets in the calyx and surface. However, the colony depicted in Verrill's Text Figure 2 is more like the holotype of *A. grandiflora* and not of a colony of *L. anitorkilda* n. gen., n. sp. There is no way to confirm exactly which specimen (or specimens?) Verrill figured in this paper, however it is possible it may not have been the holotype of *A. grandiflora* or perhaps he used more than one specimen to assemble the description. Additionally, this current research has confirmed that of the specimens listed as *A. grandiflora* in Madsen (1944) three are valid but one specimen ('Thor' Stat 168) is an example of the new species *L. anitorkilda* n. gen., n. sp.—another instance of the confusion of the two species.

The variation observed amongst specimens of *A. grandiflora* shows the holotype to be a specimen with minimal complexity in the warts and tubercles of the sclerites and in the shape of the sclerites themselves. Nevertheless, the tangled colony form, long thin spatulate clubs in the pinnules and generally simple tuberculate spiny-spindles with a tendency to be clavate seem to be consistent characteristics across the specimens examined. At this stage there are not enough consistent differences to reliably delimit other species within the sample set, however considering the large geographic range which is currently recorded for this species and the diversity within other deep-sea genera it would not be surprising if future studies can confidently define other *Anthothela* species within this group.

A. grandiflora appears to be reasonably wide-spread in the deep waters of the Atlantic Ocean. *Anthothela tropicalis* and *Anthothela quattriniae* n. sp. also occur in the Atlantic, although *A. quattriniae* n. sp. is currently only recorded from the Gulf of Mexico. Both of these species have large thorn clubs, bulbous in *A. quattriniae* n. sp., and both have colonies with very prickly surfaces with the thorn clubs projecting outwards. *A. grandiflora* lacks true thorn clubs and has a relatively smooth surface. *Anthothela pacifica* has currently only been recorded from the northern Pacific Ocean and has small, straight spiny-spindles and clubs in the calyces and cortex which are smaller than those recorded in *A. grandiflora.*

Specimens of another species herein assigned to *Anthothela*, *A. vickersi*, carry the same haplotype as specimens of *A. grandiflora* using two mitochondrial gene regions (mtMutS and igr1–COI) (see section 2.3.3). However, the morphological and geographical differences between these populations were deemed enough to maintain separation into two species. Chiefly, the sclerites in the calyx of *A. vickersi* are large, bent thorn clubs which project out from the calyx (Figs. 2.18; 2.24), while the smaller sclerites in the calyx of *A. grandiflora*, although at times complex, do not consistently have spear tips which project out of the colony. Additionally *A. vickersi* has short, relatively broad, tuberculate rods that are common in the cortex and long, narrow spiny-spindles in the tentacle rachis and pinnules both of which are not common in *A. grandiflora;* the branches of the colonies of *A. vickersi* are not as narrow or flexible as *A. grandiflora;* and *A. vickersi* has been recorded from southern Australia and New Zealand while *A. grandiflora* is only known from the Atlantic Ocean.

Anthothela aldersladei n. sp. from Western Australia differs from *A. grandiflora* by having short, bent and spiky thorn clubs in the calyces and cortex, giving the colony a very spiky appearance, and has very large sclerites in the points (relative to the polyp head) (Figs. 2.43; 2.46).

***Anthothela pacifica* (Kükenthal, 1913)**

(Figs. 2.13–2.16)

?*Sympodium armatum* Nutting 1909: 686 (see Kükenthal 1913: 221).

Clavularia pacifica Kükenthal, 1913: 221, 237–239, Figs. e–g; Hickson 1915: 543; Kükenthal 1916: 456; Williams 2000: 338.

Scleraxonia (Briareidae?) Molander 1929: 18.

Anthothela pacifica ? author unknown; Bayer 1961: 70; Fautin, Siebert & Kozloff 1987: 70 (“shallow subtidal”).

Material examined:

Lectotype (here designated): ZMB 6304, La Jolla, China Point, California, USA, depth 92 m, 1912 (colony remains & fragment of single polyp).

Other material: fragment of **USNM 57981**, Strait of Georgia, 4 Mile NE of Entrance Island, British Columbia, Canada, depth 350 m, 14th August, 1973.

Description:

Colony form:

Unfortunately, there is nothing remaining of the syntype lodged at the museum in Warsaw, Poland (MZW 49), only the sponge on which it grew. No further mention is made of this syntype.

The lectotype is a tiny, encrusting colony growing on a small cream sponge (Fig. 2.13A, B). The piece of sponge is approximately 20 mm long and 15 mm wide with the octocoral colony growing on only a small part of it. The colony is difficult to discern on the very similar coloured sponge but there are very few remaining polyps and they are quite damaged. Three polyps are grouped close together at one end of the sponge. They appear to be attached to one another via stolons and a spreading membrane as mentioned by Kükenthal (1913), with no discernable branching or elevation of polyps off the surface of the sponge.

Colour:

Kükenthal (1913) states the colour as light yellow.

Polyps and calyces:

Calyces are prominent and approximately 2 mm tall (Kükenthal mentioned 2.5 mm tall) with a thin layer of sclerites (Fig. 2.13C). Some appear to have rounded longitudinal furrows but they are not pronounced. In most of the remaining polyps, the polyp body is partly retracted such that the base of the polyp head rests on the lip of the calyx, hiding the polyp neck. The polyp heads are approximately 1.5–1.7 mm wide and in those polyps where the bodies can be seen are approximately 1.5–2 mm tall (2.5 mm tall in Kükenthal's description). There are some smaller polyps, possibly juveniles (0.9 mm wide and 1.2 mm tall). The tentacles fold over the mouths of the polyps forming eight distinct furrows on the polyp head and a star-shaped apex to each polyp. The number of pinnules per tentacle was not determined.

Medulla:

No medulla evident.

Sclerites:

All polyps, calyces and colony surface are covered in a dense layer of sclerites, chiefly spiny-spindles. Sclerites on the polyp head are in a clearly defined collaret and points arrangement (Fig. 2.13D). At the collaret, sclerites are basically transverse but grade *en chevron* up the points to be arranged longitudinally in the distal part. These sclerites are short, straight or only slightly curved rodlets and spindles with fairly sparse, conical tubercules (Fig. 2.13F). The lengths of the sclerites are 0.1–0.3 mm (mostly 0.1–0.2 mm) only, making them significantly smaller than those found in other *Anthothela* species.

Distal from the points, sclerites continue longitudinally to obliquely along the aboral side of the tentacles (Fig. 2.13E). They are curved rodlets and spindles with sparse, conical tubercles (Fig. 2.13G) and they grade in size from largest at the proximal end of the tentacle to smallest distally and seem to curve around the side of the tentacles. Tentacle sclerites are 0.14–0.34 mm long which again is smaller than the range found in other *Anthothela* species but the ranges do overlap.

In the pinnules are found very short, almost squat, spatulate clubs, with a narrow handle and a flattened, wide tip and numerous short rods (Fig. 2.14A). The spatulate tip is oriented distally in the pinnules and some of them have quite well developed ‘teeth’ or jagged edges. Spatulate clubs range from 0.09–0.16 mm only—much smaller that the equivalent spatulate clubs in *A. grandiflora* where the range is 0.26–0.5 mm. The rodlets are short, narrow, with simple, small tubercles and are also crowded longitudinally in the pinnules (Fig. 2.14A). They range in size from 0.06–0.18 mm.

On the calyx, sclerites are arranged at all angles in a relatively thin but crowded layer. Sclerites again are straight, short rods and spindles with sparse tubercles, ranging in size from 0.16–0.34 mm (Fig. 2.14B). One straight club with a thickened distal tip was found (Fig. 2.14Ba), which corresponds to a sclerite figured by Kükenthal (1913), although he states it is from the top part of the polyp.

No samples were taken of a pharynx, so the presence, absence or nature of sclerites in the pharynx remains undocumented.

Surface sclerites are a mixture of two sorts; simple, short, straight, tuberculate rods and spindles (0.07–0.18 mm long) (Fig. 2.14C) and longer, straight spiny-spindles, mostly smooth or with minimal tubercles, sometimes with forked ends (0.13–0.24 mm long) (Fig. 2.14D). The latter are reminiscent of the sclerites found in the medulla of other species of *Anthothela*.

Variability:

A small fragment of the specimen USNM 57981 was examined. The whole colony form has four narrow branches emanating from a membranous base with some anastomoses evident; it has no main stem and calyces are distributed throughout but also tend to form terminal bunches (Fig.

2.14E). An additional fragment has well-defined ridges obvious on the calyces and most of the polyps are partly retracted so only the top part of the polyp head is visible in the mouth of the calyx (Fig. 2.14F). The fragment examined was a small branch tip with a few polyps crowded together (Fig. 2.15A). The tallest polyp is partly extended and is 1.5mm tall and 1.6 mm wide (Fig. 2.15B) while the calyces are approximately 1.5–2.5 mm tall and 1.5–1.8 mm wide. Under a dissecting microscope the sclerites are opaque and white and they are brown under transmitted light, perhaps indicating the specimen was originally fixed in formalin. There is slight damage evident in some of the sclerites. The fragment available for examination is small and the only medulla portion available is affected by the junction of a polyp so it is impossible to be definite regarding coelenteric canals penetrating the medulla and even the expected boundary canals are distorted and difficult to discern. Nevertheless it is clear there is an axial medulla and a cortex.

The pinnules have numerous spatulate clubs, many having a long, narrow handle with a wide, flattened spatulate tip, and they are longer than those of the lectotype (0.12–0.22 mm); but there are also some short, squat spatulate clubs similar to the lectotype (Fig. 2.15C). The small, narrow rodlets from the pinnules are of similar length in this specimen (0.04–0.18 mm) as in the lectotype. The tentacles have mostly curved, short, narrow tuberculate rods, arranged longitudinally on the aboral side of the rachis (Fig. 2.15D). These are very similar to the lectotype in form and length (0.14–0.35 mm). Sclerites in the points are long tuberculate spiny-spindles, slightly curved or straight (Fig. 2.15E), plus some straight sclerites with a clubbed, thorny tip (Fig. 2.15Ea) which are not obvious in the sample from the lectotype. Most point sclerites are significantly larger than those from the lectotype (0.19–0.68 mm cf. 0.1–0.28 mm). This specimen had a low number of sclerites in the pharynx, mostly short, simple flanged spindles varying in length from 0.07–0.19 mm (Fig. 2.16A). Most of the sclerites from the calyx are simple tuberculate spiny-spindles (Fig. 2.16B) although there are some clavate sclerites which resemble the clubbed sclerite from the lectotype (Fig. 2.14Ba). These are all a similar size to the lectotype at 0.14–0.38 mm long. The cortex sclerites are similar to those from the calyx although with fewer clavate sclerites (Fig. 2.16C). Most of the cortex sclerites are 0.12–0.24 mm long but there are also longer sclerites, up to 0.44 mm long. Occasionally, straight clubs are found in both the cortex and the calyx. As mentioned above, there is very little true medulla available in the fragment investigated. The medulla sclerites shown here are likely to be a mixture of surface and medulla sclerites (Fig. 2.16D).

Distribution:

In deep water off the west coast of USA and Canada, specifically southern California, USA and Strait of Georgia, Canada

Williams (2000) defines the distribution for *Clavularia pacifica* as “southern California (Monterey Bay to San Diego County)”. This includes the specimens identified as *Sympodium armatum* by Nutting (1909).

Depth:

90–350 metres.

Remarks:

At this stage, it has not been possible to confirm when and who proposed *Clavularia pacifica* should be reassigned to *Anthothela*. Molander (1929) simply listed *C. pacifica* as “Scleraxonia (Briareidae?)” with no accompanying reasons or discussions. No further mention has been found in the literature until Bayer (1961) where, in the remarks of his description of *Anthothela tropicalis*, simply stated that *A. pacifica* (Kükenthal) is a sister species to *A. tropicalis*. There is no discussion regarding why or when Bayer believed *C. pacifica* had been reassigned to *Anthothela*. Currently *Clavularia pacifica* is still listed as a valid species in some international databases and Williams (2000) mentions *C. pacifica* in a comparison with the new species *Cryptophyton goddardi* Williams, 2000.

There is so little remaining of the ZMB lectotype specimen (and nothing left of the MZW syntype) that the placement of *A. pacifica* is difficult to confirm. At this stage I contend it should be in *Anthothela* as a distinct species, but I do this with some reservation. There are no branches in the lectotype to be able to examine the arrangement of coelenteric canals in a medulla and the spatulate clubs in the pinnules are much smaller than those normally observed in other *Anthothela* species. However, some of the main defining characteristics of *Anthothela* are evident in the lectotype—the presence of (albeit small) spatulate clubs in the pinnules; all other sclerites as tuberculate spiny-spindles with some clavate; sclerites arranged as collaret and points on the polyp head; sclerites arranged longitudinally on the tentacle rachis and in the pinnules; and the presence of a calyx. Although there is no evidence of branches there are what are traditionally considered medulla sclerites present in the sample taken of the surface sclerites, perhaps indicative of the ability to form a medulla. All these points support the placement of this specimen in *Anthothela* but do not preclude alternative placements.

The specimen determined as *A. pacifica*, USNM 57981, does have a colony consistent with *Anthothela* plus it has distinctive long spatulate clubs in the pinnules. This makes the placement of this specimen in *Anthothela* unambiguous. The uncertainty regarding the placement of *A. pacifica* thus becomes more a question of whether the USNM specimen and the lectotype are the same species and how they differ from other *Anthothela* species. This decision is hampered by the size of the very small fragment of the USNM 57981 specimen available for examination here and its poor condition (possibly formalin affected).

In the lectotype, the sclerites in the pinnules are spatulate clubs but the handles are markedly shorter than those found in any other *Anthothela* species thus far described. In fact, all the sclerites from the lectotype are, on average, shorter than their equivalents in other *Anthothela* species. In Kükenthal's (1913) drawing (Figure E) he displays the sclerites as very small in relation to the size of the polyp, arranged haphazardly up the calyx and polyp body. The size difference is noticeable with average calyx sclerite length in the *A. pacifica* lectotype at 0.25 mm while the average length is 0.33 mm in *A. grandiflora* (Sars, 1856).

Other than average size, the sclerites of the lectotype are not markedly different from those found in *A. grandiflora* except for the single straight club found in the calyx (Fig. 2.14Ba). Kükenthal also figures a sclerite like this but states it is from the top part of the polyp. In this study, only one such sclerite was located in the tiny sample taken of the calyx of the lectotype and they are similarly uncommon in the USNM 57981 specimen.

I contend the lectotype of *A. pacifica* and the USNM 57981 specimen are conspecific, and given the relatively similar geographic location of the two specimens, the small sclerites and the presence of the straight clubs, this species can be distinguished from other *Anthothela* species. Nevertheless, the validity of this species remains questionable due to the paucity of type material and the condition of the other available material. Further material from the type location may be able to resolve this question, particularly using molecular differentiation.

The specimen which Nutting determined as *Sympodium armatum* and was synonymised with *Clavularia pacifica* by Kükenthal was not available for investigation here. However, another specimen, collected from the same station on the same day and placed in *A. pacifica* by Bayer in the Smithsonian collection (USNM 49519), was found to be too badly affected by formalin to be confidently assigned. It has slightly larger sclerites in the calyx and some curved and bent thorn clubs are present suggesting it may not be *A. pacifica*.

***Anthothela vickersi* (Benham, 1928) new combination**
(Figs. 2.17–2.28)

Spongioderma (?) vickersi Benham, 1928: 81–83, Figs. 25–31.

Homophyton vickersi van Ofwegen, L. (2013). Accessed through: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetails&id=288708 on 2013-VI-20.

Material examined:

Holotype: OMNZ IV8728, 21 miles north of Doubtless Bay, east coast of the North Island, New Zealand, H.M.C.S. *Iris,* col. Lieut. Vickers, depth 945 m, 1926–1928.

Other material: TMAG K3984, S-Tasmania Slope (~1000 m), Huon Commonwealth Marine Reserve (CMR), SW Tasman Sea, Australia, CSIRO RV *Southern Surveyor,* stn. 9, sample 23 (SS200702/009-023), 44.154–44.162°S, 147.128–147.131°E, depth 800–920 m, 31st March 2007; **TMAG K3985**, Hill U seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO RV *Southern Surveyor,* stn. 15, sample 38 (SS200702/015-038), 44.322°S, 147.181–147.185°E, depth 1100–1200 m, 1st April 2007; **TMAG K3986**, Z9 Seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO RV *Southern Surveyor,* stn. 58, sample 53 (SS200702/058-053), 44.202–44.199°S, 147.318–147.320°E, depth 1020–1100 m, 7th April 2007; **TMAG K4264**, Dory Hill seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO RV *Southern Surveyor,* stn. 49 (SS199701/49), 44.322–44.34°S, 147.115–147.072°E, depth 1167 m, 29th January 1997; **TMAG K4109**, Hill J1 seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO RV *Southern Surveyor,* stn. 40 (SS199701/40), 44.243–44.273°S, 147.36–147.323°E, depth 1024–1548 m, 27th January 1997; **TMAG K4110**, U (R) Hill seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO RV *Southern Surveyor,* stn. 41 (SS199701/41), 44.318°S, 147.115°E, depth 1314 m, 28th January 1997; **TMAG K4111**, Dory Hill seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO RV *Southern Surveyor,* stn. 48 (SS199701/48), 44.313–44.34°S, 147.142–147.073°E, depth 1456 m, 29th January 1997; **TMAG K4112**, Hill A1 Reserve seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO RV *Southern Surveyor,* stn. 62 (SS199701/62), 44.328–44.322°S, 147.268–147.325°E, depth 1261–2253 m, 30th January 1997; **TMAG K4113**, Hill V seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO RV *Southern Surveyor,* stn. 67 (SS199701/67), 44.393–44.387°S, 147.147–147.23°E, depth 1614 m, 31st January 1997; **TMAG K4114**, Hill V seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO RV *Southern Surveyor,* stn. 69 (SS199701/69), 44.397–44.398°S, 147.147–147.178°E, depth 1262–1854 m, 31st January 1997; **TMAG K4265**, Mongrel seamount, Huon CMR, SW Tasman Sea, Australia, stn. J2-386-06, sample 01, 44.254°S, 147.115°E, depth 982 m, ROV JASON deployed from the U.S. RV *Thomas T. Thompson,* team led by Dr Jess Adkins & Dr Ron Thresher, 23rd December 2008; **MNHN IK-2009-535**, Ile Amsterdam, Southern Indian Ocean, N/O *Marion Dufresne*, stn. 2 (JASUS, MD50, stn.2, CP07), 37.783°S, 77.65°E, depth 940–1680 m, 9th July 1986; **MNHN IK-2009-534**, Ile Saint Paul, Southern Indian Ocean, N/O *Marion Dufresne*, stn. 23 (JASUS, MD50, stn.23, CP113), 38.917°S, 77.633°E, depth 1065–1125 m, 19th July 1986; **NIWA 40439**, Macquarie Ridge, NE of Macquarie Island, Southern Ocean, NIWA RV *Tangaroa*, stn. 77 (TAN0803/77), 53.738°S, 159.114°E, depth 1014–925 m, 11th April 2008; **NIWA 40508**, Macquarie Ridge, NE of Macquarie Island, Southern Ocean, NIWA RV *Tangaroa*, stn. 79 (TAN0803/79), 53.715°S, 159.131°E, depth 770–810 m, 12th April 2008; **NIWA 40578**, Macquarie Ridge, NE of Macquarie Island, Southern Ocean, NIWA RV *Tangaroa*, stn. 81 (TAN0803/81), 53.731°S, 159.166°E, depth 1150–1270 m, 12th April 2008; **NIWA 41129**, Macquarie Ridge, S of Macquarie Island, Southern Ocean, NIWA RV *Tangaroa,* stn. 118 (TAN0803/118), 59.048°S, 158.901°E, depth 1400–1615 m, 19th April 2008; **NTM CO12800**, North Macquarie Ridge, NE of Macquarie Island, Southern Ocean, CSIRO RV *Southern Surveyor,* stn. 97 (SS199901/97), 53.932°S, 159.098°E, depth 364 m, 26th January 1999; **NTM CO12801** (ex TMAG K1398), North Macquarie Ridge, NE of Macquarie Island, Southern Ocean, CSIRO RV *Southern Surveyor,* stn. 120 (SS199901/120), 53.645°S, 159.158°E, depth 1050 m, 30th January 1999

Description:

Colony form:

The holotype is a piece of a larger colony, and is approximately 60 mm long and 3–4 mm in diameter (Fig. 2.17A, B). There is a sharp bend approximately in the middle of the branch. Benham (1928) states that the colony “had been put into a phial too narrow and too small for it, so that the stem is bent and some of the branchlets are broken off”. There are one or two small circles where the cortex of the colony is missing and the medulla is visible—these may be the origins of the branchlets mentioned by Benham, although they could also be evidence of broken polyps (Fig. 2.17Ba). One end of the main branch is slightly flattened and broadened where there once was a side branch (Fig. 2.17Bb). There are two small side branches remaining, each emanating close to the sharp bend in the colony. One side branch is 13.3 mm long and 3.3 mm wide (Fig. 2.17Aa) while the other is simply a polyp bunch and is 10 mm long (including the length of the terminal polyp) and 11.5 wide (which includes two transversely arranged polyps). The main branch is approximately circular in cross-section although slightly distorted at bifurcation points where it tends to be elliptical. There is no evidence of membranous parts of the colony or anastomoses.

One side of the colony appears to be clear of polyps but this is an artefact of the storage conditions where the colony was secured to a glass slide for many years. Most of the polyps which were on that side of the colony have been bent aside or broken off (Fig. 2.17A cf. Fig. 2.17B). The calyces are arranged on all sides without order. They occur close together throughout the colony, with the largest distance between polyps at 4 mm, and are particularly crowded or clumped at the tip of the side branches with no free surface between them.

Grossly, the colony is in reasonably good condition with approximately 30 intact polyps and 18 empty calyces. The surface of the colony is mostly complete and undamaged.

Colour:

According to Benham, the colony was “a pale colour” but he is clearly describing it sometime after preservation given he mentions the distortion of the colony due to limited space in the “phial”. It is now light beige in alcohol.

Polyps and Calyces:

Calyces are mostly cylindrical, sometimes taller than wide, and are usually at right angles to the branches except for those at the branch tips which tend to extend at oblique angles from the branch (Fig. 2.18A) and they range from 2.3–4.5 mm high and 2.4–3.5 mm wide. The exsert part of the polyps varies from approximately 2.2–4.5 mm tall; most are partly retracted so the polyp head rests on the lip of the calyx (Fig. 2.18B) but one or two polyps are somewhat extended so the polyp neck is partly visible (Fig. 2.18C). There are no fully retracted polyps although there is one polyp which only projects very slightly. Tightly crowded sclerites occur throughout with those on the polyp head arranged as points and a collaret and those on the calyces having the tips projecting out from the surface, giving the calyces a prickly appearance (Fig. 2.18B, C). The tentacles in most of the polyps are folded over into the polyp mouth and so form a rounded mound with eight furrows. According to Benham there are 4–6 “long and narrow” pinnules along each side of the tentacles.

Medulla:

The branches are composed of a thin cortex surrounding a medulla composed of sclerites tightly packed together. Sclerites are arranged longitudinally to obliquely in both the medulla and cortex. In a cross-section of the axis, a ring of longitudinal boundary canals distinctly separates the cortex from the medulla (Fig. 2.19A). These canals run parallel and close to one another but do not appear to frequently anastomose. Thus the boundary canals do not form a true boundary space. There are no obvious coelenteric canals occurring in the central medulla. Two small cross-sections were made from one cut end of the central branch only, so there was no opportunity to assess the occurrence of central coelenteric canals throughout the colony. In one of the cross-sections, in the centre of the medulla the density of the sclerites thinned slightly giving an indistinct impression of a central canal. Benham (1928) describes and depicts the boundary canals and later states “it [the medulla] presents no canals, but a few small sub-circular spaces occur towards the centre, which I take to be due to spicules having dropped away”.

Sclerites:

Many of the sclerites are in good condition; however those sclerites where the tips projects out from the colony (mostly from the calyx and the top of the points) are smooth and rounded. On close investigation, the sclerites have a slight fuzziness around the perimeter of their projecting tip and the tip is brown while the remainder of the sclerite is clear (Fig. 2.19B). Sclerites which do not project from the surface do not have this feature. Given the nature of similar sclerites from identical regions in other species, it seems most probable that the projecting tip of these sclerites have had their thorny or foliaceous ornamentation eroded leaving only slight rounded isolated bumps, perhaps by a short immersion post-mortem in an acidic medium. The damaged sclerites are figured, however caution is necessary when comparing with sclerites from other *Anthothela* species.

The collaret consists of many transversely arranged sclerites which grade *en chevron* up the points to be longitudinal in the distal part with many sclerites bunched together and projecting slightly past the aboral side of the infolded tentacles (Figs. 2.18B; 2.19C). Point and collaret sclerites consist chiefly of long, narrow, straight or slightly curved spiny-spindles with relatively simple tubercles (Fig. 2.20) and assumed thorn clubs with smoothed tips (Fig. 2.20a). The simple spindles range in length from 0.11–0.96 mm while the thorn clubs are 0.27–0.56 mm long. The distinct distal tips of the thorn clubs project out from the polyps. There are also rare small crosses and flanged spindles arranged amongst the larger sclerites.

Between the well-defined points, a small number of intermediate sclerites occur, arranged in a narrow line with the ends of the sclerites slightly overlapping each other (Fig. 2.18Ba). They are narrow, tuberculate spindles similar to those found in the points.

The aboral face and the sides of the tentacles are covered in a dense layer of crowded sclerites all arranged longitudinally or obliquely (Fig. 2.19C) with some sclerites projecting above the surface, giving the tentacles a prickly appearance. Most of the tentacle sclerites are short, straight rods with simple, relatively sparse tubercles (Fig. 2.21A). Some of the sclerites have a slight hook or curl at one tip where they curve around the side of the tentacles. Most of these sclerites range in size between 0.1 and 0.4 mm long but there are also very small sclerites which appear to be from the distal end of the tentacles where they tend to jumble together and mix with the sclerites in the pinnules. Additionally there are rare, short, thorny clubs which appear to be mixed in with the other sclerites—these are approximately 0.15–0.46 mm long (Fig. 2.21B).

The pinnules are packed with many long, narrow spatulate clubs and spiny-spindles arranged longitudinally with the spatulate end of the clubs in the distal tip of the pinnules (Fig. 2.22). The spatulate tips are sometimes not well-developed, with some sclerites lacking a markedly splayed end (Fig. 2.22a). Sizes ranges from 0.2–0.52 mm long with no obvious order to the arrangement of the different sizes within the pinnules. There are also small, straight spiny-spindles in the pinnules (Fig.

2.22b) which range from approximately 0.08–0.25 mm long. Additionally, there are long, narrow sticks, usually straight, with sparse tubercles (Fig. 2.22c) which range from 0.3–0.6 mm long. These appear to extend down into the pinnules but can also be concentrated along the sides of the tentacles.

In the pharynx there are small spindles and rods with simple tubercles usually arranged in girdles (Fig. 2.23A). Most of the sclerites are 0.04–0.20 mm in length. The sclerites tend to be grouped in indistinct longitudinal lines in the pharynx which correspond to the insertion of the mesenteries (Fig. 2.23B). The sclerites are not crowded.

The calyces are covered in a dense layer of sclerites, many of which project from the surface giving them a prickly appearance (Fig. 2.18B). A large proportion of the sclerites from the calyx are thorn clubs with an irregular distal tip which appears to be damaged or partially dissolved as mentioned previously (Fig. 2.24a). The sclerites appear to have unaffected warts and tubercules on the proximal end with some of these being quite complex. Most of these sclerites are slightly curved and are 0.29–0.62 mm long. There are other sclerites also present in the calyx, seemingly unaffected, which include many spiny-spindles, 0.18–0.6 mm long, with numerous tubercles, some clubbed sclerites (0.28–0.33 mm long) and short flanged spindles (0.11–0.18 mm long; Fig. 2.24b).

The cortex has rough, knobbly patches created by densely occurring tuberculate sclerites (Fig. 2.18A). The sclerites are mostly short, stout tuberculate rods and longer, narrower spindles (Fig. 2.25A). The short rods are approximately 0.12–0.28 mm long while the spindles are from 0.2–0.5 mm long. In the only cortex sample taken, a single sclerite was found which could be considered a true thorn club, apparently undamaged (Fig. 2.25Aa). It is a possible contamination from the calyces or there may be rare thorn clubs in the cortex. Benham (1928) states the surface "presents a coating of obliquely and irregularly-disposed, short, knobby spicules, very densely fitted together, and below them occur longitudinally-disposed, long, thorny spindles." This layering may simply be the distinction between cortex and medulla.

Sclerites from the medulla also tend to be of two forms; warty spindles and sparsely tuberculate rods and spiny-spindles (Fig. 2.25B). The small sample of medulla taken for this re-description has many broken sclerites so their length is difficult to estimate, however Benham (1928) described "long spindles with thorny outgrowths and, the short knobbly rods". Here the (mostly unbroken) warty spindles range from 0.2–0.5 mm long while the (mostly broken) sparsely tuberculate rods are 0.13–0.44 mm long. It is likely the tuberculate rods can be much longer. There is evidence of fusing and branching of the sclerites.

The sclerites are all translucent and colourless under transmitted light except for the damaged tips of the projecting sclerites which are brown.

Variability:

The apparent degradation of the tip of the thorn clubs in the points and calyx of the holotype hinders a definitive diagnoses of the species but given factors such as the gross morphology of the colony, general sclerite architecture and geographic proximity many specimens are here determined as conspecific with the holotype. The assumption is that the rounded tips are an anomaly restricted to the holotype, and the clubs would have once resembled the thorn clubs found in recently collected specimens presented here. If future fresh samples from the type location have similar rounding of the thorn clubs it may be considered a natural feature of the species and determinations herein should be reassessed.

Most of the specimens examined are reasonably consistent with the holotype. In all the samples, long, narrow sticks are arranged along the sides of the tentacles and extend into the pinnules, joining the long spatulate clubs longitudinally in the pinnules (Fig. 2.26Aa). These sticks are often more frequent than in the holotype but otherwise the tentacle sclerites have similar form to those of the holotype (Fig. 2.26Ba, C). All specimens have thorn clubs in the points (Fig. 2.27A) and calyx (Fig. 2.27B) with more developed thorns and spines on their pointed tip compared with the damaged tip of those in the holotype. Additionally, in the Tasmanian seamount samples, the short, tuberculate rods in the cortex often have one clubbed or pointed, smoothed tip (Fig. 2.28Aa) which is not common in the small sample taken of the holotype surface.

Some of the specimens have a large number of long, well-developed thorn clubs in the cortex. The small sample of the holotype cortex had only a single large thorn club but further sampling may have found more given the prickly appearance of the colony surface.

Photographs taken shortly after collection of specimens from the Tasmanian seamounts suggest the live colour is light creamy pink (Fig. 2.28B, C). The Tasmanian seamount specimens are all relatively small suggesting the species does not grow particularly large. However, in situ photographs taken on the Tasmanian seamounts suggest it is a reasonably common species, with many colonies of what is presumed to be *A. vickersi* (based on quantity collected, light creamy pink colour and general colony form).

Distribution:

Northern New Zealand and the seamounts south of Tasmania, Australia; Southern Indian Ocean.

Depth:

800–1600 metres.

Remarks:

When discussing the holotype, Benham acknowledged the lack of relevant literature available to him and his sparse knowledge of the group, and admitted he placed the specimen in the genus *Spongioderma* "with much hesitation". He in fact included a question mark in the original designation ("*Spongioderma (?) vickersi"*). It has remained in this now defunct genus mainly due to lack of any comprehensive review of the related taxa and an uncertainty as to the whereabouts of the holotype. Fortunately, the holotype could be located and re-described and it can now be confirmed as a species of the genus *Anthothela*, based on the spatulate clubs crowded in the pinnules, boundary canals separating the cortex from the medulla, no or indistinct canals in the medulla and sclerites which are chiefly tuberculate, often clavate spiny-spindles. This specimen thus represents the first valid record of a species of *Anthothela* in the southern hemisphere. Unfortunately, defining the species is more problematic due to the assumed damage to the tips of the projecting sclerites. The cause of this partial dissolution of the sclerites is unknown. In Benham's description there is no mention of the medium in which the specimen was originally preserved. He mentions "poor preservation" when discussing the boundary canals but does not elaborate. He also states that the "projecting points are covered with a thin stainable membrane, the mesogloea" and that the "column [calyx] is provided with short, stout, round-ended rods with many rounded knobs". This suggests the brown, rounded, fuzzy tips on the calyx sclerites were present when Benham was originally describing the specimen and thus the damage may have already occurred. The sample was removed from an old, sealed jar for this re-description. It was found to be in 50% ethanol with trace amounts of benzene.

Nevertheless, *A. vickersi* can be distinguished from other species included in *Anthothela* by the presence of the very long and narrow sticks with sparse tubercules in the tentacle rachis and pinnules, (presumed) thorn clubs in the calyx and numerous, short, stout tuberculate rods in the cortex. This differs from *A. tropicalis,* which has many large and bent thorn clubs in the cortex and *A. quattriniae* n. sp. which has large bulbous thorn clubs. *A. aldersladei* n. sp. has a preponderance of short thorn clubs in the cortex and very large spindles in the points and collaret. *A. pacifica* and *A. grandiflora* do not have the bumpy surface or prickly calyces evident in *A. vickersi*.

Specimens of *A. grandiflora* carry the same haplotype as specimens of *A. vickersi* using two mitochondrial gene regions (mtMutS and igr1–COI) (see section 2.3.3). However, the morphological and geographical differences between these populations were deemed enough to require separation into two species. *A. vickersi* has been recorded from southern Australia and New Zealand while *A. grandiflora* is only known from the Atlantic Ocean. The sclerites in the calyx of *A. vickersi* are large, bent thorn clubs which project out from the calyx, while the sclerites in the calyx of *A. grandiflora*, although at times complex, do not consistently have spear tips which project out of the colony. Additionally, *A. vickersi* has short, relatively broad, tuberculate rods common in the cortex and long, narrow sticks in the tentacles and pinnules which are not common in *A. grandiflora* and the branches of the colonies of *A. vickersi* are not as narrow or flexible as those in colonies of *A. grandiflora*.

Anthothela tropicalis **Bayer, 1961**

(Figs. 2.29–2.38)

Anthothela tropicalis Bayer, 1961: 68, Fig. 13.

Material examined:

Holotype: fragment of **USNM 50650**, southeast of Galveston, Texas, Gulf of Mexico, Oregon stn. 534, 27.533°N, 93.027°W, depth 732-823 m, 11th April 1952.

Other material: fragment of **USNM 1090549**, St. Augustine, Reed Peak #160, North Atlantic Ocean, 29.849°N, 79.633°W, depth 742-828 m, 9th Nov 2005.

Description:

Colony form:

Only a tiny fragment of the holotype was examined for this study (Fig. 2.29E) so parts of the original description have been incorporated here (Bayer 1961). According to Bayer, originally the holotype was a rambling colony with "crooked" branches forming a "tangled mass" with no central stem; he figured only a small fragment (Fig. 2.29A). The holotype now consists of six fragments (Fig. 2.29B); four of these are straight to slightly bent pieces of branch and two are pieces of tangled branch with anastomoses evident. There is no central stem or obvious holdfast. There are many calyces present but very few remaining polyps. The calyces apparently were "widely separated on all sides" but no distances between calyces or measurements of colony surface without polyps were given. On the holotype fragments, calyces are evident on all sides of the branches and distributed evenly throughout. There is no mention or evidence of clumps of polyps which is a common feature in other species of *Anthothela*. The fragment examined is 1.9–2.1mm in diameter (which corresponds with "about 2.0 mm" from Bayer) and is basically circular in cross-section.

Colour:

According to Bayer, "the colonies (sic) are ivory white in alcohol". The fragment examined here is also white in alcohol. There is no mention of live colour.

Polyps and calyces:

Calyces, as described by Bayer, are cylindrical in shape, “about 1.5 mm tall” and 2–3 mm wide from his figure (Fig. 2.29A). Bayer does not give the dimensions of polyps in the text but from the figure the head of the polyp extends approximately 2 mm from the lip of the calyx and is 1.8–2 mm wide. Most of the polyps were preserved exsert although Bayer mentions that the “polyps are fully retractile” and in his figure a polyp head is partly retracted such that the base of the polyp head rests on the lip of the calyx (Fig. 2.29A). One of the few remaining polyps visible on the holotype fragments resembles that figured by Bayer (Fig. 2.29Ba).

The fragment examined here has mound-shaped calyces which are approximately 1.2 mm tall and 2 mm wide with no discernable ridges. The polyp is fully retracted within its calyx and appears poorly developed—it may in fact be a juvenile polyp (Fig. 2.29Ca). The calyces and the colony surface are covered in large sclerites which have a projecting tip giving the colony a very prickly appearance (Figs. 2.29D). The polyp head has sclerites arranged in a distinct collaret and points (Fig. 2.30A) and the tentacles are folded tightly into the mouth forming eight mounds and furrows, giving the top of the polyp a starred appearance. A single row of approximately 10 pinnules appear to be arranged along each side of the tentacles but it was impossible to accurately determine the number of pinnules with the material available.

Medulla:

Bayer included a figure of a cross-section of the colony (Fig. 2.29Aa), and a cross-section from the fragment of holotype here generally confirms this figure (Fig. 2.30B). The branch consists of a medulla of tightly packed sclerites, longitudinally or obliquely arranged, surrounded by a thin cortex. The cortex and the medulla are separated by a series of longitudinal canals, running adjacent to each other and so close as to form a circle of boundary canals. They are, however, still discernible as individual canals and do not appear to frequently anastomose. There is no evidence, either in Bayer’s figure or the small cross-section taken here, of internal coelenteric canals within the medulla. However, Bayer qualifies his description by admitting that the “material is not sufficiently well-preserved to determine the extent to which the medulla is penetrated by solenia”. There is insufficient material to investigate the canal arrangements any further.

Sclerites:

The polyp head is covered in closely packed sclerites, with approximately 10 transverse rows of sclerites forming a collaret and others arranged *en chevron* to longitudinally in eight points. These sclerites (0.2–0.87 mm long) are mainly curved or straight spiny-spindles with relatively simple tubercules (Fig. 2.31). Occasionally, there are sclerites where one end has more developed spines and projections and these are positioned in the points such that the tips project above the base of the folded tentacles (Fig. 2.32). It was impossible to adequately determine the arrangement of the sclerites on the polyp neck due to the limited material available.

The tentacles are crowded with sclerites that are arranged longitudinally along the back and angled obliquely on the side. They are mostly short tuberculate spiny-spindles, usually straight, sometimes curved, and are approximately 0.1–0.4 mm long (Fig. 2.33B). Bayer mentions that the tentacle sclerites have “spines larger at one end than elsewhere” and includes them in his figure (Bayer, 1961 Fig. 13a). A few sclerites like those figured were found in this study (Fig. 2.33Ba) although they were not the dominant sclerite type in the tentacles. However, not specifically mentioned by Bayer is the fact that the pinnules are packed with longitudinally arranged spatulate clubs with an enlarged and flattened distal tip along with some simple small spiny-spindles and rods particularly in the distal tip of the tentacle (Fig. 2.33A). Sclerites from the pinnules range in size from 0.06–0.35 mm long, with the spatulate clubs falling mainly into the range of 0.19–0.35 mm long.

Bayer mentions that the pharynx has “numerous slender, spinose spindles about 0.1 mm long”. In this study sclerites were found to be very numerous and densely arranged throughout the pharynx, leaving very little free tissue (Fig. 2.34A, B). They are small, slender spindles with sparse, small tubercles, approximately 0.05–0.12 mm long (Fig. 2.34C).

The calyces and cortex are covered with tightly packed, relatively large sclerites which project outwards, making the calyces and colony surface very prickly (Fig. 2.29D). These sclerites are termed “bent hockey-stick spindles” by Bayer but conforming to the much later published octocoral glossary (Bayer et al. 1983) they are here termed thorn clubs, and they have a spear-like tip that projects up or out from the surface. They are usually bent or curved but not exclusively and are mostly covered in simple to quite complex warts and tubercules (Figs. 2.35A; 2.36A). The spear-tips are mostly smooth with foliose or flattened spines and little or no tuberculation. These thorn clubs range in length from 0.28–0.68 mm long in the calyx. In the cortex, the thorn clubs tend to be of similar size (0.33–0.78 mm long) but there are more numerous small ones (Fig. 2.36A). Mixed in with the thorn clubs, in both the calyces and cortex, are straight or slightly curved tuberculate spiny-spindles (Figs. 2.35B; 2.36B). These range in length from 0.18–0.6 mm long in the calyx and 0.33–0.57 mm in the cortex where they appear to be more common. This is supported in Bayer’s description where he states “in the cortex [the bent hockey-stick spindles] are smaller and many ordinary spindles are mixed with them”.

Sclerites from the medulla are mostly long, narrow spiny-spindles with sparse, simple tubercules (Fig. 2.37). Occasionally, there are large sclerites with a greater covering of tubercules or warts. In the small sample taken here the sclerites ranged from 0.32–0.66 mm long, although Bayer mentions that the medulla sclerites often exceed “a length of 0.5 mm”. There is evidence of sclerites occasionally fusing and branching.

The sclerites were all translucent and colourless under transmitted light.

Variability:

The tiny fragment of USNM 1090549 examined consists of only three polyps arranged as a terminal branch cluster (Fig. 2.38). The sclerites differ slightly from the holotype in having more numerous thorn clubs in the points. The polyps and calyces are taller and narrower than those from the holotype (calyx 2.2 mm high with the polyp fully extended 3.4 mm above that; polyp head 1.6 mm wide) but the colony has the spiky surface characteristic of *A. tropicalis* and the other sclerites correspond with those of the holotype. However, it does not have the densely arranged sclerites in the pharynx that the holotype does but this characteristic may not be of any taxonomic use. This specimen is from the east coast of Florida.

Distribution:

Gulf of Mexico; northern Atlantic Ocean off the coast of Florida, USA

Depth:

732–828 metres.

Remarks:

Regretfully, there are very few polyps remaining on the holotype, and only a tiny fragment was available for study. Nevertheless, further specimens are likely to be collected in the future. In fact, in Bayer’s description he mentioned “colonies are white in alcohol” so although he only explicitly mentioned and figured the holotype he appeared to have more than one specimen at his disposal. Of the specimen USNM 1090549, a similarly small fragment was available for study. Unfortunately, with so little material available, the phylogenetic importance of calyx and polyp form and size is impossible to assess. Geographic proximity and the presence of large thorn clubs in the calyx and cortex are the main features tying these specimens together. Future research, particularly molecular results which were not possible for these specimens, may also assist with this species delineation.

Distinguishing *A. tropicalis* from other species in *Anthothela* is dependent on the presence and, in fact, dominance of thorn clubs in the calyx and surface. *A. grandiflora* has, at times, quite complex sclerites in the calyx but it does not have the true thorn clubs with smooth, sharply pointed tips. Consequently, the surface and calyces of *A. grandiflora* are not as thorny as those of *A. tropicalis*.

Additionally, sclerites in the pharynx are always sparsely arranged in *A. grandiflora* while those in the *A. tropicalis* holotype are crowded with little sclerite-free tissue in the pharynx. Finally, Bayer mentions that in *A. tropicalis*, the polyps are "widely separated on all sides". This might be considered a difference with other *Anthothela* species which all tend to have polyps closely bunched and, at times, quite crowded.

A specimen collected from a location very close to that of the holotype of *A. tropicalis* is herein described as the new species *A. quattriniae* n. sp. It too has thorn clubs in the calyx and surface of the colony but these thorn clubs are bulbous and swollen, particularly in their mid-section (Fig. 2.60). Bayer compares *A. tropicalis* with *A. pacifica*, calling them "a twin pair", one from the Pacific Ocean and one from the Gulf of Mexico. He claims *A. tropicalis* has "smaller and more numerous spicules in the crown and a broader collaret". In fact, the lectotype of *A. pacifica* has very small sclerites, in general much smaller than those of *A. tropicalis*. Using the limited material from both type specimens it appears *A. pacifica* lacks the large, bent thorn clubs of *A. tropicalis*, instead having straight clubbed sclerites in the calyx and points.

A. aldersladei n. sp. has thorn clubs dominant in the calyx and surface but they are usually shorter than those in *A. tropicalis* (0.19–0.54 mm cf. 0.33–0.78 mm). In the surface of *A. aldersladei* n. sp. the small thorn clubs are almost exclusive with very few straight, regular sclerites as opposed to *A. tropicalis* which has a far higher percentage of regular tuberculate spiny-spindles mixed in with the thorn clubs. Additionally, *A. aldersladei* n. sp. has very large points and collaret sclerites relative to the size of the polyp. At this stage, *A. aldersladei* n. sp. has only been recorded from the Indian Ocean, in waters off Western Australia.

A. vickersi is a very similar species to *A. tropicalis*. It has similar sized thorn clubs in the calyx but they only rarely occur in the surface. The surface sclerites of *A. vickersi* are a mixture of straight, tuberculate and warty spiny-spindles with numerous short, rounded clubs with a slightly developed tip which *A. tropicalis* lacks. Additionally, *A. vickersi* has only been recorded from the southern Pacific Ocean.

***Anthothela aldersladei* sp. nov.**

(Figs. 2.39–2.52)

Material examined:

Holotype: WAM Z31463, 190km NW of Karratha, Pluto Gas Field, Western Australia, SKM Pluto Gas Field Survey (PF06/S1–600/R2), 19.874°S, 115.166°E, depth 600 m, 7th December 2005

Paratype: WAM Z13059, North West Cape, Exmouth, Western Australia, AIMS North West Cape Survey II 2002, Fromont, J., Marsh, L.M. & Alderslade, P.N., stn. 04, 21.48°S, 113.966°E, depth 570 m, 20th March 2002

Description:

Colony form:

The holotype is broken into 6 small, irregular pieces of branches, all with calyces and polyps (Fig. 2.39A). It is not possible to confidently reconstruct the shape or size of the colony, however the slightly twisted nature of the branches and the many bifurcation points indicate the colony form was probably tangled with irregular branching. The pieces of colony range in length from 10.6 mm to 24.6 mm and all are narrow (1.2–2.2 mm) and relatively delicate. The branches are usually circular in cross-section although tend to flatten or distort at bifurcation points and where calyces arise. One piece has some evidence of anastomoses. All the colony pieces are in good condition with many intact polyps and undamaged surfaces.

On three of the colony pieces, calyces are crowded into clavate terminal bunches with no space between the bases (Fig. 2.39B). Proximal to the terminal bunches and on the remainder of the colony pieces, calyces occur sparsely, on all sides of the branches and projecting at right angles. There are sections of the branches which have no calyces; the largest of these spaces is 8.8 mm long.

Colour:

There is no record of live colour for this specimen; it is now light beige in alcohol.

Polyps and Calyces:

Calyces are large relative to the branch diameter and range from 1.5–2.5 mm in height and 2–2.5 mm in width. They tend to be conical and are clearly differentiated from the polyp neck and head by the arrangement and alignment of the sclerites (Fig. 2.40A), which are small, crowded, arranged longitudinally and project out from the surface of the calyx giving it a prickly appearance. In contrast, immediately above the calyx lip, on the polyp neck and head much larger sclerites are arranged transversely, covering the polyp neck with no obvious thinning of the dense arrangement as is usually the case in other *Anthothela* species. These large sclerites continue obliquely to longitudinally up eight well-defined and quite spectacular points. All polyps are extended with little or no invagination of the neck region and often with the polyp head bent over (Fig. 2.40B), protruding 2.2–3.2 mm from the lip of the calyx and having heads of approximately 1.2–2.2 mm in diameter. The eight tentacles fold over the mouth of the polyp creating eight rounded ridges on the top of the polyp head. There are approximately 10 pinnules arranged in a single row along each side of the tentacles.

Medulla:

The branches of the colony are composed of a central medulla, made up of tightly packed longitudinal sclerites, which is surrounded by a cortex that is approximately 0.1–0.2 mm thick. The cortex and medulla are separated by a crowded series of adjacent longitudinal canals which encircle the medulla allowing it to be easily separated from the cortex. A cross-section taken at the widest available part of the branches clearly shows the boundary canals, but in the medulla there are no obvious, internal coelenteric canals (Fig. 2.41A). In a narrower part of the colony, another cross-section demonstrates the same clear boundary canals with perhaps some indistinct canals in the central medulla (Fig. 2.41B) which are more likely a thinning of the sclerites rather than defined canals. The body cavities of the polyps along the branches terminate at the medulla while the gastric canals of the polyps that are arranged in bunches at the tips of some branches tend to extend internally down the branch a short distance.

Sclerites:

The polyps and calyces are covered with a dense layer of crowded sclerites which are mostly spiny-spindles on the polyp head and spiky thorn clubs on the calyx and colony surface. On the polyp head sclerites are very large, relative to the polyp, and are not as crowded as elsewhere on the colony. The largest sclerites are bent or curved tuberculate hockeystick spindles, with the straight, longest part of the sclerite arranged longitudinally in the points and the proximal portion curving to be transverse at the base of the points (Figs. 2.40A; 2.42). Some have roots (or small branches) at the base and many have a serrated, thorny tip (Fig. 2.43) that are arranged distally in the points and can project out from the polyp head and above the back of the folded tentacles (Fig. 2.42). There is no true collaret, rather sclerites extend transversely and obliquely down the polyp neck with no diminution of the sclerite cover at the neck area. Sclerites in the points range in size from 0.40–0.90 mm approximately while those from the neck (lacking the different distal tips) are slightly smaller (0.26–0.77 mm).

From the tip of the points, sclerites continue obliquely along the back of the tentacles (Fig. 2.44). These sclerites are bent or straight tuberculate rods and spiny-spindles often with one curved end (Fig. 2.45Aa) which bends around the side of the tentacle extending down towards the pinnules. Straight sclerites are more commonly on the middle ridge of the tentacle rachis. The sclerites grade in size along the tentacle; on the proximal end, the largest sclerites are approximately 0.58 mm long grading to the distal end of the tentacle where the smallest sclerites are approximately 0.20 mm long.

In the pinnules, sclerites are crowded longitudinally and are delicate and easily broken (Fig. 2.44). Flat spatulate clubs are common, with a tapered handle and a widely spread, spatulate, almost leaf-like end, arranged distally in the pinnules (Fig. 2.45B). These sclerites vary in length from 0.12–0.32 mm and the handle can be narrow and cylindrical or wide and flat. The smaller sclerites grade from spatulate clubs to simple tuberculate rods. There are also short flat rods with sparse tubercules (0.08–0.1 mm long) and narrow curved spiny-spindles (0.14–0.21 mm long) inter-dispersed with the spatulate clubs (Fig. 2.45C, D).

Calyces are covered in a dense and prickly layer of sclerites, almost all of which are small, bent, tuberculate thorn clubs (Fig. 2.46), orientated with the foliaceous, thorny tips distal on the calyx and angled out from the surface giving the calyx its prickly appearance. For the smaller sclerites there is some gradation between thorn clubs and sclerites which are less developed at the tip and could be termed a wart club. Most calyx sclerites range from 0.22–0.52 mm, however there are some smaller, straight, tuberculate spiny-spindles, mingled with the thorn clubs, which only reach approximately 0.17 mm in length.

Very small sclerites with tall conical tubercles occur in the pharynx (Fig. 2.47A). They are quite numerous and tend to occur in bunches. The size ranges from 0.05–0.12 mm long.

The cortex contains sclerites very similar to those in the calyx—small, bent, tuberculate thorn clubs with quite complex, at times foliose, spear-tips (Fig. 2.47B). They are tightly packed with the tips projecting out from the surface giving the branches a very prickly appearance. Size does not vary much with most of the sclerites being from 0.19–0.43 mm long but occasionally there are some up to 0.53 mm long and as small as 0.12 mm. Amongst these short thorn clubs are some simple, tuberculate spiny-spindles of similar lengths but the thorn clubs are far more common.

The medulla is composed of tightly packed, longitudinally arranged sclerites—mostly sparsely tuberculate spiny-spindles (Fig. 2.48). Occasionally there are larger spiny-spindles with only sparse warts, often with branches, forks and fused areas. Most sclerites are from 0.20–0.53 mm long although many of these showed evidence of breakage. It was difficult to ensure these long sclerites remained undamaged during sampling so the prevalence of these cannot be estimated. Occasionally there were small flanged spindles only 0.1 mm in length.

Sclerites are uniformly transparent under transmitted light.

Variation:

The paratype, WAM Z13059, is membranous only, thinly encrusting large, straight sponge spicules (Fig. 2.49A, B). It is from a site close to where the holotype was collected and was found at a similar depth. There is a similarly obvious delineation between the calyx and the polyp body (Fig. 2.49B, C) but no retracted polyps were noted. Straightened out, the largest polyp is 5 mm long with the head 1.7 mm long and 1.4 mm wide. The sclerites on the points and neck region are smaller than the holotype (the largest measured at 0.58 mm) and slightly more crowded (Fig. 2.49C, D) but the serrated ridges and thorny tubercles on the distal tips of the point sclerites resemble those of the holotype (Fig. 2.50A) as do those sclerites from the neck (Fig. 2.50B). Between each group of point sclerites there are two small intermediate sclerites which are narrow, curved spindles (Fig. 2.50C). The arrangement of sclerites in the tentacles is similar to that in the holotype (Fig. 2.51A) with hooked tuberculate rods (Fig. 2.51B) arranged obliquely along the aboral side of the tentacle rachis, diminishing in size towards the distal tip and pinnules packed with spatulate clubs arranged longitudinally (Fig. 2.51C). Some small spindles with sparse, simple tubercles were found in the pharynx (Fig. 2.51D). The calyces have well-developed, foliose thorn clubs similar to the holotype (Fig. 2.52A) which project out from the surface giving it a prickly appearance (Fig. 2.49Aa). The basal membrane of the colony contains predominantly small spindles, up to 0.2 mm long (Fig. 2.52B). The larger spindles and leaf-clubs shown in the lower part of this figure were not common, and are most likely from the region where the membrane merged with the base of a polyp.

Distribution:

Western Australian coast

Depth:

570–600 metres

Remarks:

This species is different to other species in the genus *Anthothela* in having such large sclerites on the neck and in the points and predominately small thorn clubs in the calyces and surfaces.

The paratype is membranous only. Colony form has been such a large part of historical determinations in octocorals that linking this colony with scleraxonians which are predominantly branched is not immediately intuitive. In the absence of a medulla, the presence of spatulate clubs in the pinnules, obvious calyces and clavate sclerites can provide a trigger to assess specimens with regards to *Anthothela.* Sclerite form and type are a crucial part of this decision and an assessment of inter- and intra-specific variation of sclerites is fundamental. Unfortunately, with only two specimens of this species such a species-level assessment is difficult.

It was only possible to obtain successful sequences of the two mitochondrial gene regions mtMutS and igr1–COI from the holotype. Across the length of the two gene regions combined there was only a single nucleotide different from a clade consisting of *A. grandiflora* and *A. vickersi* specimens (see section 2.3.3). In the phylogenetic analysis this was sufficient for the *A. aldersladei* n. sp. specimen to be positioned outside the *A. grandiflora/A. vickersi* clade but with low support. A single nucleotide in a single specimen may be no more than sequencing error so further attempts to sequence other specimens are necessary for a more robust result.

Etymology:

Named in honour of my incomparable PhD supervisor, Dr Philip Alderslade who originally recognised the paratype as a possible *Anthothela* species and used the specimen as the catalyst for this revision.

Anthothela quattriniae **sp. nov.**

(Figs 2.53–2.64)

Material examined:

Holotype: fragment of **USNM 1207951**, Gulf of Mexico, USA, Lophelia II, L11–10–464, JASON ROV, J2-531 GB535, 27.426°N, 93.589°W, depth 522 m, 20–21st October 2012

Description:

Colony form:

The holotype is a tangled colony with narrow branches and no central stem, and is approximately 80 mm high and 90 mm wide (Fig. 2.53A). A number of small pieces of the holotype were examined for the description (Fig. 2.53B). The pieces consist of six fragments of the colony, all with polyps and calyces arranged along narrow branches. The pieces range in size from 6–23 mm long and 4–14.5 mm across at the widest parts (Fig. 2.53B). The largest piece has six bifurcations with no distinguishable order or arrangement. The arrangement of the branches (combined with evidence of missing branches obvious at a number of places) indicates there were anastomoses present when the colony was whole. Branches are circular to elliptical in cross-section and range from 0.6–2.2 mm wide; there is some distortion of the branches at the bifurcation points and where the calyces occur. There is no holdfast or evidence of encrusting colony in the fragments examined but in the photograph of the whole colony it appears to be attached to a solitary coral and possibly has more than one attachment point (Fig. 2.53A).

Calyces and polyps occur along and around all of the branches. The largest space between two calyces is approximately 2 mm but most are closer than that, and they are crowded together at the branch tip, making it clavate (Fig. 2.54A, B).

The colony is in good condition with many intact polyps and the cortex complete.

Colour:

Soon after collection the colony was recorded as white. The fragments of the holotype examined are white in alcohol.

Polyps and calyces:

Calyces are low cylinders, with height and width about the same, projecting usually at right angles from the branches and bearing large projecting sclerites (Fig. 2.55A). There are many smaller, probably juvenile polyps and calyces mixed amongst the larger ones (Fig. 2.54A, B)—the larger calyces are approximately 1–2 mm high while the juveniles are approximately 0.6–1.0 mm high. Calyces tend to be as wide or slightly wider than they are tall with larger calyx widths ranging from 1.5–2.5 mm (juvenile calyces between 1–1.5 mm wide). Calyces have a very rough, prickly appearance due to the projecting sclerites and, although there are not true longitudinal ridges on the calyces, there is a slight tendency for the largest projecting sclerites to be arranged in longitudinal columns with the sclerites between the columns tending to be smaller.

Most polyps are partly retracted so the base of the polyp head sits on the lip of the calyx and the polyp neck is not visible (Figs. 2.54B; 2.55A). These polyps extend approximately 1–1.5 mm from the lip of the calyx with the juvenile polyps extending only 0.5–0.8 mm. Occasionally there are polyps fully retracted within the calyces with just a small round aperture obvious at the apex of a pyramidal calyx (Fig. 2.55B). These calyces are approximately 1–1.2 mm high. Only one polyp in the holotype fragments examined is slightly extended, and this is only on one side of the polyp, otherwise there are no extended polyps. Polyp heads are approximately 1–2 mm wide and are crowded with large sclerites arranged into a collaret and points (Fig. 2.55A, C). Large, spectacular sclerites project up from the points above the flat top of the polyp, which is formed where the tentacles fold over the mouth of the polyp. Thus the polyp heads have imposing spiky peaks with the distinction between the points and the back of the tentacles being quite pronounced. There is a single row of 12 pinnules along each side of the tentacles.

Medulla:

The colony branches have a central medulla surrounded by a thin cortex. Both the medulla and cortex are comprised of tightly packed sclerites arranged longitudinally or obliquely. A ring of coelenteric canals, running longitudinally along the branches, surrounds the medulla, clearly separating it from the cortex (Fig. 2.55D). The canals are adjacent to each other but do not seem to anastomose or join thus they are always discernable as separate canals. They do not form a true boundary space. There are no obvious canals in the medulla.

The bodies of the polyps arranged along the branches truncate in a flat base at the medulla while the polyps at the branch ends are slightly more elongated with the gastric cavities extending internally down the branches a small distance.

Sclerites:

A robust covering of sclerites encase the colony pieces. Polyp heads have an impressive spiky crown formed by large, more or less longitudinally arranged sclerites in the points, which grade from *en chevron* to transverse at the base of the polyp head to form a stout collaret, approximately 5–6 large sclerites in depth. The most common sclerite type in the collaret and the base of the points is straight or slightly curved spiny-spindles with simple tubercules (Fig. 2.56). These sclerites mostly grade from 0.5–0.7 mm long. At the top of the points there are large, bulky thorn clubs projecting above and away from the polyp head. These sclerites (Fig. 2.57) have a short, warty handle and a long, large head. The lower part of the head is bulbous and commonly narrows to a long, thorny, distal point. The handles are reasonably crowded with complex warts while around the bulbous middle of the sclerites there are only low and fairly simple tubercles. The distal tips, which are easily damaged while handling the colony, have foliaceous spines and smooth tubercles. Most of these bulky thorn clubs range in length from 0.45–0.8 mm although there are smaller ones only reaching approximately 0.3 mm long. On the single polyp which has some neck exposed, the neck region is covered in similar sclerites to the collaret, all transversely arranged. These are still quite large and crowded, surprisingly so considering the polyps can invaginate into the calyces.

At the top of the polyp head where the tentacles fold over, there is an abrupt change in the form of the sclerites. The bulky thorn clubs from the points give away to slightly curved rods, with simple tubercules, arranged almost *en chevron* along the aboral side of the tentacle rachis (Fig. 2.58A). These sclerites tend to curve over the side of the tentacles and they grade down to small rods arranged haphazardly at the very tip of the tentacles (Fig. 2.58B). These sclerites grade continuously from 0.1–0.4 mm long.

The pinnules are tightly packed with longitudinally arranged, narrow sclerites (Fig. 2.59). The most distinctive type of sclerite in the pinnules is the spatulate club. They are long and narrow with a flattened spatulate tip positioned distad in the pinnules (Fig. 2.58A) and range from 0.1–0.3 mm in length. There are also small, straight, narrow sclerites with sparse, small tubercles and some flattened rods also with sparse tubercules; both these groups range from 0.07–0.25 mm long.

The calyces have two distinctive types of sclerite. Firstly, large bulbous thorn clubs, some with rounded distal tips, some with spear tips, project out from the calyx giving it a very prickly, complex surface (Fig. 2.55A). Many of these clubs are bent with the projecting, foliaceous tip of the sclerites arranged distally in the calyx. These sclerites have quite complex, crowded warts, particularly on the handle while the head has smooth tubercules and spines (Fig. 2.60). There are also bulbous sclerites which do not have a spear tip although they are less common (Fig. 2.60a). All these large sclerites are 0.4–0.6 mm long. The other type of calyx sclerite is a much smaller spiny-spindle with simple to complex tubercules, some with only slightly expanded distal tips or with spear tips (Fig. 2.61) and are only 0.1–0.4 mm long. All sclerites are mixed together on the calyx except for just below the lip where the large, bulbous sclerites cease and only the smaller sclerites are present, arranged haphazardly (Fig. 2.55A).

Small (0.5–0.15 mm long), narrow sclerites with sparse lateral spines and warts occur in the pharynx (Fig. 2.62A). Overall they are not prolific; however they tend to occur more densely in line with the mesenterial attachments than in between (Fig. 2.62B).

The large bulbous clubs extend from the calyx onto the surface of the branches, resulting in the same prickly appearance for the spaces between the calyces. These sclerites however, tend not to have the pointed, foliaceous tip of the thorn clubs but more commonly are rounded, swollen sclerites covered in large, complex warts (Fig. 2.63A). The rounded ends of the sclerites project out from the surface of the colony. There tends to be a gradient from the largest bulbous sclerites, with the dense covering of complex warts (approximately 0.2–0.43 mm long), to narrower spiny-spindles, also with complex warts, right through to long spiny-spindles with simple tubercles (approximately 0.2–0.57 mm) (Fig. 2.63B). These sclerites are mixed together in the cortex with no discernible order to their placement.

The medulla sclerites resemble the simple sclerites from the cortex. There is a mixture of straight spiny-spindles with sparse, simple tubercules through to complex warts (Fig. 2.64). Most of the sclerites with sparse tubercules range from 0.17–0.5 mm long but there are larger sclerites, up to 0.8 mm long. The sclerites with more complex warts and knobs range from 0.2–0.4 mm long.

The sclerites were all translucent and colourless under transmitted light.

Distribution:

Gulf of Mexico, USA

Depth:

522 metres

Remarks:

This specimen was first separated from the other *Anthothela* specimens using molecular results shared with me by Andrea Quattrini (Temple University, USA). Subsequent morphological investigation supported this separation due to the distinctive bulbous sclerites present in the calyx and surface of this specimen, not found in any other *Anthothela* species. Characteristics of the genus *Anthothela* are present such as the spatulate clubs crowded in the pinnules, spiny-spindles placed longitudinally (to *en chevron*) along the aboral side of the tentacle rachis, adjacent boundary canals separating the medulla and cortex, no internal medullary coelenteric canals and multiple anastomoses.

It is probably most closely related to the sympatric species *Anthothela tropicalis* which also has thorn clubs in the calyx and cortex. The holotypes from both *A. tropicalis* and *A. quattriniae* n. sp. were collected from very similar locations. However, the bulbous nature of the thorn clubs in *A. quattriniae* n. sp. distinguishes the species from *A. tropicalis* which has narrow, pointed thorn clubs (see Fig. 2.60 cf. Fig. 2.35). The size of sclerites may also be informative, however unfortunately the fragment of the holotype of *A. tropicalis* examined here is very small, has many broken sclerites, and has only a single polyp so comparisons of size of polyps and sclerites are prone to possible misinterpretation. No other specimen examined displayed the bulbous sclerites of *A. quattriniae* n. sp. Unfortunately, no specimens which conform to the morphological definition of *A. tropicalis* were available for molecular studies but future comparisons of DNA sequences from *A. quattriniae* n. sp. and *A. tropicalis* may be elucidatory. There are likely to be other specimens from the Gulf of Mexico available for comparison and these would assist in defining intraspecific differences within *A. quattriniae* n. sp. and thus better delineating it from *A. tropicalis*.

Other known *Anthothela* species all lack the bulbous spear-spindles present in *A. quattriniae* n. sp.

Etymology:

The species was named in honour of Andrea Quattrini, a fellow student from Temple University, California, USA, who recognised specimens she was working on were potentially *Anthothela*, and then shared these specimens and their DNA sequences with me.

***Victorgorgia* López-González and Briand, 2002**

Victorgorgia josephinae López-González & Briand, 2002: 98.

Diagnosis:

Arborescent monomorphic scleraxonians with sparse, irregular branching, generally in one plane; anastomoses absent or rare; medulla extensively penetrated by large, well-defined coelenteric canals and separated from a thin cortex by a boundary space formed by anastomosing boundary canals; calyces distributed all over most of the colonies, crowded at the branch tip; pinnule and tentacle sclerites include josephinae clubs and tuberculate spiny-spindles; sclerites from points, calyx, cortex and medulla are mainly tuberculate spiny-spindles; pharynx lacks sclerites.

Type species: *Victorgorgia josephinae* López-González & Briand, 2002 by monotypy.

Remarks:

Herein three species of *Anthothela* (*A. argentea* Studer, 1894, *A. macrocalyx* (Nutting, 1911) and *Clematissa alba* Nutting, 1908 (=*A. nuttingi* Bayer, 1956)) are transferred and two new species are added to the genus *Victorgorgia.* An amended diagnosis of the genus was necessary to accommodate the additional species. Additional illustrations of the type species *V. josephinae* were also necessary to assist in the delimitation of these species. A form of sclerite common in the genus, 'josephinae clubs', is defined in the 'Terminology and taxonomic characters' section within (see section 2.2.3).

Victorgorgia josephinae López-González & Briand, 2002

(Figs. 2.65–2.66)

Victorgorgia josephinae López-González & Briand, 2002: 97–105, Figs. 1–6**.**

Material examined:

Holotype: MNHN OCT.2008-0004, Josephine Bank, SW of Portugal, Victor cruise, PL 28/05, 37.8°N, 14.017°W, depth 1500 m, 14th August 1998.

Description:

The holotype is in good condition and the characteristics of the colony, calyces, polyps and sclerites are as that described by López-González & Briand. The sclerites from the back of the tentacles are almost exclusively josephinae clubs (Fig. 2.65A). They are arranged with the clubbed tip distad and projecting out from the tentacle, as pictured in Fig. 2D–F of López-González & Briand's description. The pinnules are crowded with longitudinally positioned, straight, narrow, sparsely tuberculate spiny-spindles and clubs along with smaller josephinae clubs that are less-developed than those in the tentacle rachis (Fig. 2.65B). According to López-González & Briand, the sclerites from the tentacles range from 0.19–0.48 mm long which generally concurs with measurements taken here (0.16–0.43 mm long). The authors did not distinguish between sclerites from the back of the tentacles and those from the pinnules.

All other sclerites in the holotype are well-represented in the figures of López-González & Briand's description excepting those from the calyx. The latter do not significantly differ from those found in the points and collaret and in the cortex (López-González & Briand (2002) Figs. 6A; 5B respectively), consisting of straight, tuberculate spiny-spindles without clavate or modified tips (Fig. 2.66). The size range is 0.35–0.57 mm long.

Remarks:

The description and figures in the original form a functional portrayal of *Victorgorgia josephinae* and do not need significant revision. However, a more extensive figure of pinnule and tentacle sclerites from the holotype is necessary to assist in the delineation of *V. josephinae* from the newly added species.

The so called "hockey-stick" sclerites in the tentacles (Fig. 6B of López-González & Briand and Fig. 2.65A here) are common in the genus and an important part of the delimiting features of this species. However, these sclerites do not match those pictured as "hockeystick spindles" in Bayer et al. (1983) so herein they have been named josephinae clubs.

Other species in this genus are distinguished from *V. josephinae* mainly by sclerite differences. The three species transferred to *Victorgorgia* have only fragmented holotypes thus a comparison of colony form is not possible. *V. alba* (*=A. nuttingi*) and *V. macrocalyx* have squat rods on the back of the tentacles and very few josephinae clubs while *V. argentea* has large, straight, dense clubs in the top of the points and along the back of the tentacles. Of the new species added to the genus herein, *V. eminens* n. sp. is magenta to deep purple (while *V. josephinae* is cream with purple polyps) and has simple, tuberculate spiny-spindles on the back of the tentacles mixed with only a few josephinae clubs, and *V. nyahae* n. sp. has spiky thorn clubs in the back of the tentacles and in the calyx.

Victorgorgia argentea **(Studer, 1894) new combination**

(Figs. 2.67–2.76)

Anthothela argentea Studer, 1894: 60.

Material examined:

Holotype: MCZ 4219, off the west coast of Mexico, U.S. Fish Commission Steamer '*Albatross*', stn. 3430, 23.267°N, 107.517°W, depth 1559 m, 19th April 1891.

Other material: MCZ 51046, Off Oahu, 20km W of Makaha, Hawaii, T.A. Clarke collection, depth 1200 m, 5th Sept 1977.

Description:

Colony form:

The colony was originally described by Studer (1894) as having a "forme arborescente, les branches naissent d'un tronc principal sous des angles presque droits", translated as having the form of a tree, with branches arising from one main trunk at almost right angles. However, the dried holotype is now in 8 pieces with some additional small fragments (Fig. 2.67A). Two of the largest pieces are straight portions of branch with polyps scattered along the length. One of these is 66 mm long with a diameter of 3.4 mm at the widest point where it is slightly flattened (Fig. 2.67B). For most of the length, the branch is basically circular in cross section (approximately 2.6 mm diameter) although polyp bunches tend to cause some distortion. There is no evidence of side branches. The second fragment of branch is 62.7 mm long with a diameter of 4.2 mm at the widest point and 3.1 mm at the narrowest. There is evidence that there were two side branches on this piece, both of which have broken off at their base. Both ends of these two fragments are broken and they cannot conclusively be placed to form a larger branch. There is no evidence of anastomoses. Most of the other fragments of the holotype are terminal bunches of crowded polyps (Fig. 2.67C). The colony fragments and the many attached polyps are in reasonable condition although extremely brittle. There are also a number of loose polyps. A small piece of the holotype was re-hydrated for this project.

Calyces with exsert polyps are tightly crowded in bunches at the branch tip (Fig. 2.67C) as well as being distributed irregularly along and all the way around, and generally at right angles to the branches. The largest distance between calyces is approximately 7 mm but more commonly they are closer together, in some sections touching. Occasionally, there are isolated calyces with polyps.

Colour:

In the original description, Studer noted the colour of the colony to be white in alcohol, as it is now for the dried fragments. There is no record of the live colour of the colony, however Studer indicated that the large sclerites on the back of the tentacles were glassy and silvery in colour against a background brown hue of the tentacles and the re-hydrated fragment fits this description. Some of the sclerites are brown and fibrous when magnified under transmitted light, which combined with the silvery appearance, indicated the original preservation was in an acidic media, probably formalin.

Polyps and calyces:

Calyces are flat-topped, conical shaped and range in height from 1.5–2.4 mm. The polyps are relatively large, extending up to 2.5 mm from the calyx with a head diameter of between 2.2–3.4 mm (Fig. 2.68A). Sclerites on the calyx are arranged *en chevron* at the base becoming longitudinal towards the lip. Most of the polyps are exsert, although often contorted or bent, likely attributable to jar storage. No polyps are fully retracted into the calyces, although some are retracted to such an extent that the polyp head sits on the top lip of the calyx and the polyp neck is hidden. The tentacles in some polyps are extended but bunched (Fig. 2.68B) while others have the tentacles folded over the mouth such that the top of the polyps is an eight–lobed mound (Fig. 2.68C). There are approximately 8–10 pinnules arranged in a single row along each side of the tentacles.

Medulla:

The fragile, brittle nature of the dry holotype prohibited the dissection of the branches to fully investigate the arrangement of the internal coelenteric canals. However, the broken ends of the colony pieces allow confirmation of the presence of a central medulla, consisting of tightly packed, mainly longitudinally arranged sclerites, surrounded by a narrow cortex, similarly consisting of crowded sclerites (Fig. 2.68D, E). A boundary space can be seen to clearly separate the thin, loosely attached cortex from the medulla. The medulla has two or three large and obvious canals (0.3–0.5 mm diameter) positioned approximately in the centre (Fig. 2.68D, E). These significant canals are obvious at the proximal end of the colony fragments as well as just below the polyp bunches on the ends of the branches, suggesting they extend throughout the colony.

Sclerites:

The polyp heads are well protected by being covered in crowded sclerites which are predominately long, warty spiny-spindles arranged as points and a bulky collaret. In the points, the sclerites are arranged *en chevron*, bunched so they are layered over each other (Figs. 2.67C; 2.68A). They are straight or slightly curved tuberculate spiny-spindles, between 0.46–0.81 mm long (Fig. 2.69A); tubercles are predominantly simple, blunt-topped or rounded cones. Among these are large, opaque, thick, prickly, club-shaped sclerites, approximately 0.45–0.77 mm long (Fig. 2.70). These occur more commonly in the distal part of the points and some of them continue longitudinally for a short distance along the back of the tentacles with the thickened blunt ends arranged distad (Figs. 2.68A–C; 2.69B). They are usually straight although some bent spindles also occur (Fig. 2.70a).

The collaret is composed of long curved spindles, arranged transversely in crowded bunches of between 10–20 on the widest part of the polyp head (Fig. 2.68A) and have a comparable length to the more slender sclerites from the points. Below the collaret on the polyp neck are similar narrow, tuberculate spindles arranged mostly obliquely but more sparsely than in the collaret.

The tentacles fold over the mouth and have short, straight, thorny clubs and josephinae clubs crowded longitudinally along their aboral side (Figs. 2.69B, C; 2.71). These grade in length from approximately 0.2–0.5 mm, with the length decreasing towards the tentacle tip, and with the clubbed ends positioned distad. Somewhat crowded, conical thorns cover the clubbed sclerite tip and some of the bent tips project up from the tentacle rachis giving it a rough surface.

Similarly, the pinnules have longitudinally arranged josephinae clubs, and the clubbed ends are directed towards the tip of the pinnules (Fig. 2.69B). They are usually 0.25–0.35 mm long in the pinnules and possible smaller than this in the rachis, although delineating in size between them is largely arbitrary (Fig. 2.72). Short and sparsely tuberculate spiny-spindles and flattened rods (0.11–0.24 mm long) are also crowded longitudinally in the pinnules.

No sclerites were found in the pharynx.

In the calyx, sclerites are in a single, almost translucent layer, and arranged transversely at the base but angle upwards, becoming *en chevron* distally such that there can be indistinct peaks of sclerites on the lip of the calyx (Fig. 2.68A). The sclerites are long, mostly straight, tuberculate spiny-spindles and are usually between 0.42–0.82 mm long (Fig. 2.73), although there are some shorter smoother spindles (0.27–0.37 mm).

In the cortex, sclerites tend to be arranged longitudinally along the branch, although this arrangement is often interrupted or distorted by the calyces. They are quite crowded and form an opaque layer. Cortex sclerites are similar to the sclerites from the calyces—straight and curved spiny-spindles with simple tubercules, mixed with occasional small, smooth spindles (Fig. 2.74). They can be between 0.28–0.94 mm long but most are 0.43–0.86 mm.

The medulla is formed of tightly packed, longitudinally and obliquely placed sclerites that are most commonly long, straight or slightly bent spiny-spindles (Fig. 2.75). Amongst these are some sclerites with sparse tubercules, some with crowded, complex warts and thorns and a few that are forked and branched, however no fused medulla sclerites were observed. The majority of the sclerites are between 0.47–0.98 mm but they can reach up to 1.25 mm.

Most sclerites are translucent under transmitted light except the thick clubs from the points and tentacles which are brown.

Variability:

The only other specimen examined, MCZ 51046, has sclerites which are mostly similar to the holotype but the colony and the calyx distribution represent slight differences. The colony is in two pieces, each piece with a single bifurcation (Fig. 2.76A). The largest colony piece has a short, single stem, approximately 10 mm long which then forks into two branches, 21 mm and 35 mm long and 1.5–2.5 mm in diameter. The branches are slightly flattened in the plane of the colony and are oval in cross-section. Calyces are evenly and relatively sparsely distributed on the colony fragments, although they tend to form small clumps (maximum of 4 calyces) at the branch tip (Fig. 2.76B). The calyces mostly emerge only on the narrow, lateral edges of the oval branches. When compared with the holotype of *V. argentea*, in MCZ 51046 the calyces are further apart, with much less clumping (the holotype has multiple crowded clumps of calyces) and the colony is finer. However, without knowing exactly how the holotype parent colony was constructed it is impossible to know the significance of these differences. The calyces have a single layer of sclerites arranged in indistinct chevrons and the polyps have large clubbed sclerites arranged in the distal points and on the back of the tentacles as in the holotype (Fig. 2.76C, D). In addition, all other sclerites conform in general to those of the holotype, including josephinae clubs from the tentacles and pinnules (Fig. 2.76E).

Distribution:

The eastern Pacific Ocean (off the coast of Mexico) and the Hawaiian seamounts.

Depth:

1200–1559 metres

Remarks:

Despite the colony form and branching arrangement traditionally being of considerable taxonomic importance, Studer did not provide the colony size or an illustration, and the colony form cannot be reliably reconstructed from the pieces of the holotype. Nevertheless, Studer's description of an "arborescente" branching arrangement with a main trunk supporting side branches is sufficiently different from the characteristic tangled colony form of *Anthothela* with no central trunk and common anastomoses to be considered significant. Other features such as josephinae sclerites in the tentacles, obvious coelenteric canals in the medulla and the lack of sclerites in the pharynx mean this species cannot remain in *Anthothela* but does fit the diagnoses of *Victorgorgia.*

V. argentea most resembles *V. alba* (=*A. nuttingi*) and *V. macrocalyx,* which also have large, warty clubs in the points. The most consistent differences are the sclerites from the tentacles—both these species have thick, warty rods as the main tentacle rachis sclerite and have poorly developed (or even lack) josephinae clubs while *V. argentea* has many josephinae clubs and lack the warty rods. The presence of large, opaque clubs in the distal points and aboral side of the tentacles distinguishes this species from *V. josephinae, V. nyahae* n. sp. and *V. eminens* n. sp. Additionally, *V. nyahae* n. sp. has sharply pointed thorn clubs along the back of the tentacles and in the points.

Victorgorgia alba **(Nutting, 1908) new combination**

(Figs. 2.77–2.86)

Clematissa alba Nutting, 1908: 582, Pl. XLIV Fig. 4, XLVIII Fig. 4.
Muriceides alba Kükenthal 1924: 166.
Anthothela nuttingi Bayer, 1956: 86, Figs. 9a–e.

NOT *Anthothela alba* (=*Clavularia alba=Rhizoxenia alba*) (Greig, 1887) Molander, 1929: 18

Material examined:

Holotype: fragment of **USNM 25378,** Nihoa Island, Hawaii, RV '*Albatross*', stn. 4157, 23.08°N, 161.87°W, depth 1394–1829 m, 6th August 1902 ("off Bird Island" in original description).

Description:

Colony form:

In the original description the whole colony is described as "incomplete, about 22 mm high, consisting of a sinuous stem giving off two large unequal branches about 50 mm apart" (Nutting 1908). The height of the colony at 22 mm would be very small and appears to be an error on Nutting's part as the branches are then mentioned as 50 mm apart. The holotype is now two fragments, both of which are straight to slightly curved branches; one fragment has a single bifurcation (Fig. 2.77A), the other is a small piece of branch with a terminal polyp bunch (Fig. 2.77B). In Bayer's redescription the colony is described as "ramose; branches stout, clavate" (Bayer 1956). Bayer gives the diameter of the main stem width as 6.5 mm while the branches taper from 3.5 mm in diameter proximally to 2.5 mm distally at their narrowest below polyp clusters at the branch tip. Both authors describe the calyces as occurring on all sides of the branches (according to Nutting in an "irregular spiral") and forming crowded clusters at the branch tip. Average space between calyces is not mentioned by either author but they appear reasonably crowded right along the branch and occurring on all sides (Fig. 2.77A). For the purposes of this redescription, only a tiny piece of a branch and two detached polyp heads of the holotype were available for examination (Fig. 2.77C).

Colour:

Nutting mentions the “axis, cortex and calyces are all creamy white in color (in alcohol)” but he does not mention the live colour. Bayer mentions the colour as “ivory white throughout”.

Polyps and calyces:

Most of the polyps are partly retracted such that the base of the polyp head sits on the lip of the calyx (Fig. 2.77A, B). No polyps appear to be fully retracted within the calyces and neither Nutting nor Bayer mentions such an occurrence. Nutting lists the calyx as 5.5 mm high “to the top of the operculum” and 3 mm in width at the lip of the calyx and Bayer describes the calyces as “cylindrical and ungrooved” with no measurements. However, some calyces appear to have faint longitudinal furrows (Fig. 2.77B). At their widest point the two polyp heads available are 3.2–3.4 mm wide and 2–2.5 mm high from the top of the calyx to the top of the polyp head. The remnant of a calyx available for this study occurs at right angles to the branch, has only a single layer of sclerites arranged in a faintly *en chevron* arrangement and is quite delicate (Fig. 2.77D). In the two polyp heads available for examination and in the colony figures, the tentacles fold tightly over the polyp mouth giving the polyps a mostly flat summit with eight mounds. There are 7–9 short pinnules in a single row along each side of the tentacles.

Medulla:

The branch consists of a centrally positioned medulla, made up of tightly packed, longitudinally arranged sclerites surrounded by a cortex, also made up of a layer of packed sclerites. The cortex and medulla are clearly delineated by many, longitudinal canals forming a ring of boundary canals in cross-section (Fig. 2.78A). These canals join and anastomose together to form a boundary space which allows the cortex to easily be separated from the medulla. Additionally, there are 4–5 large and conspicuous canals running through the centre of the medulla. These range from 0.25–0.5 mm in diameter, some are circular and some are oval. Bayer states the “solenia”, which perforate the medulla near the base, “diminish and seem to disappear entirely toward the branch tips”. No further attempt to investigate the canal arrangement was possible due to the shortage of available material.

Sclerites:

The polyp head is covered in a thick layer of sclerites, arranged as a collaret and points (Fig. 2.78B). The collaret consists of approximately 8–10 transverse rows of curved to straight spiny-spindles with simple, relatively sparse tubercles (Fig. 2.79). Similar sclerites are arranged *en chevron* above the collaret, eventually becoming longitudinal at the top of the points—lengths usually range from 0.45–0.8 mm but sclerites up to 1 mm were noted. Mixed in with these at the peak of the points are large, bulky clubs with the clubbed ends arranged distally (Figs. 2.78B; 2.80). They have small warts and tubercles which are reasonably crowded, making the sclerites almost opaque. These are easily visible on the polyp head and make the eight points quite large and impressive. They are a comparable length to the simpler sclerites in the points, usually 0.45–0.95 mm.

Sclerites are arranged longitudinally in a thick layer on the back of the tentacles and decrease in size towards the tip of the tentacle (Fig. 2.81A, B). There are thick rods with blunt ends and closely crowded tubercles as well as a few rare spindles with very few tubercles and straight, smaller clubs with tubercles clumped at one end (Fig. 2.82). The thick rods are a relatively consistent length (0.22–0.44mm) and appear to be more common at the proximal end of the tentacles and in the top layer of the sclerites (Fig. 2.81B). The slightly clubbed sclerites are approximately 0.20–0.36 mm long and are more crowded in the tip and sides of the tentacles with the clubbed end arranged towards the tip of the tentacle. Finally, the mostly smooth spindles are 0.28–0.37 mm long.

Small spiny-spindles are crowded longitudinally in the pinnules (Figs. 2.81B; 2.83). Ranging from 0.09–0.26 mm long, they are lightly tuberculate, often slightly flattened, and sometimes have slightly clubbed tips with thin handles. These resemble josephinae clubs common in other species of *Victorgorgia* but are only poorly developed (Fig. 2.83a).

No sclerites were detected in the pharynx.

In the calyx, sclerites are straight or very slightly curved spiny-spindles with only a minor covering of simple tubercles (Fig. 2.84). Sclerite length grades from approximately 0.32 to 0.70 mm with no noticeable size arrangement on the calyx. There are also a few flanged spindles where a few tubercles and small flanges or thorns are situated approximately mid-way on the sclerites (Fig. 2.84a). These are shorter than the other calyx sclerites at 0.15–0.24 mm long.

Similarly, the cortex has straight spiny-spindles, although these sclerites have a more substantial covering of tubercles than those from the calyx and are, in general, larger (0.37–0.82 mm) and appear more substantial (Fig. 2.85). There are also smooth, flanged spindles like those in the calyx although these are larger, ranging in length from 0.23–0.33 mm (Fig. 2.85a).

The medulla is formed of tightly packed, longitudinally and obliquely placed sclerites that are most commonly long, straight or slightly bent spiny-spindles up to 1.25 mm long, but most are within 0.47–0.98 mm (Fig. 2.86). There are also spiny-spindles, mostly smooth but with a few simple conical tubercles, and spindles with more crowded warts. There is evidence of some fused and branched sclerites.

Sclerites are all transparent under transmitted light excepting the bulky sclerites in the tentacles and points, which have brown tinges.

Distribution:

Hawaiian seamounts

Depth:

1394–1829 metres.

Remarks:

When Bayer (1956) reassigned Nutting's species *Clematissa alba* to *Anthothela* he gave it the name *Anthothela nuttingi* because of Molander's claim that *Clavularia alba* (=*Rhizoxenia alba*) (Grieg, 1887) belonged in *Anthothela* and the resulting new combination *A. alba* (Grieg, 1887) therefore took precedence. It is now clear however, that *Clavularia alba* does not belong in *Anthothela* (see below) and had Bayer known that he could have formed the binomial *Anthothela alba* (Nutting, 1908) which would have been considered valid at the time. As has been demonstrated above, Nutting's species does not belong in *Anthothela* and so Bayer's reassignment of the species to that genus is no longer acceptable and *A. nuttingi* becomes a synonym of *Clematissa alba,* which is here transferred to *Victorgorgia,* thus becoming *V. alba* (Nutting, 1908).

The holotype of *Clavularia alba* (Greig, 1887), (originally *Rhizoxenia alba*) was examined for this study and although no polyps remain, the colony was obviously stoloniferous only, with surface sclerites quite uncharacteristic of *Anthothela*. Thus it is impossible to be definitive on where *C. alba* belongs but it is not a species of *Anthothela.*

Unfortunately, only a tiny fragment of the holotype of *V. alba* was available for examination; nevertheless, when combined with Nutting and Bayer's descriptions it can confidently be asserted that this species does not belong in *Anthothela.* The presence of large canals in the medulla and the absence of sclerites in the pharynx combine to exclude this specimen from the revised definition of *Anthothela.* These characteristics instead support the re-assignment to *Victorgorgia,* as do general polyp and sclerite form. However, similar to *V. macrocalyx*, there are very few or poorly developed josephinae clubs in the tentacles, which are common in other species of *Victorgorgia*. This may be due to limited material not revealing the sparse clubs or it may reflect truly that the clubs are absent and this specimen does not belong in *Victorgorgia.* Alternatively, it may be that the presence/ absence or abundance of the clubs is simply an interspecific variation within *Victorgorgia*.

Specimens collected from similar locations to that of the holotype would assist in defining this quandary.

There are specimens determined as *Anthothela nuttingi* that have been collected around the Hawaiian Islands (S. France and A. Baco pers.com.) and some of these specimens have DNA sequences currently available on GenBank. A fragment of one such specimen (USNM 94435) was examined and found not to correspond morphologically with the holotype of *V. alba*. Additionally, using molecular results within, USNM 94435 groups with *V. eminens* n. sp. from the Tasmanian seamounts (see section 2.3.3). Thus it is extremely likely there is more than one species of *Victorgorgia* on the Hawaiian seamounts and all samples previously determined as *A. nuttingi* require revision.

Based on what was available of the holotype, the key differences of *V. alba* from other known *Victorgorgia* species are the presence of bulky, closely warted sclerites in the points plus thick rods on the back of the tentacles and none or very few josephinae clubs. The most comparable species is *V. macrocalyx*, which unfortunately was similarly massively restricted in material available for examination. Both species have thick rods on the back of the tentacles, bulky clubs in the points and few josephinae clubs—they differ slightly in the shape and concentration of tubercles on the rods on the back of the tentacles and the bulky sclerites from the points. The *V. alba* holotype could simply be interpreted as a larger, more developed version of *V. macrocalyx.* The differences are tenuous and probably insufficient for confident determinations. However, until more specimens can be compared from the two type locations (Hawaii and Indonesia) the species must remain separate.

For the other species of *Victorgorgia; V. josephinae* and *V. argentea* can be separated from *V. alba* by their abundance of josephinae clubs and the lack of thick rods in the tentacles, *V. eminens* n. sp. by the absence of large, bulky sclerites in the points and *V. nyahae* n. sp. by the presence of sharply pointed thorn clubs.

Victorgorgia macrocalyx **(Nutting, 1911) new combination**

(Figs 2.87–2.93)

Suberia macrocalyx Nutting, 1911: 15, Pl. III Fig. 3, 3a, Pl. XI Fig. 5a–c.

Semperina macrocalyx Kükenthal 1916: 174; 1919: 51, 57; 1924: 22; Thomson & Dean 1931: 192, Pl. XIV Fig. 3, Pl. XXIV Fig. 6; Stiasny 1937: 35, 119, Pl. IV Fig. 34, Textfigure J.

Anthothela macrocalyx Verseveldt 1942: 170, Fig. 5.

Iciligorgia macrocalyx van Ofwegen, L. (2013). Accessed through: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetails&id=742687 on 2013-X-26.

Material examined:

Holotype: fragments of **ZMA COEL 3280,** near Menado, Celebes, Indonesia, *Siboga* Expedition, stn. 122, 1.975°N, 125.158°E, depth 1264–1165 m, 17th July 1899.

Description:

Colony form:

In his description, Nutting describes the holotype as an incomplete specimen consisting of an "erect stem with short scattered branches" that is 135 mm in length (Nutting 1911) (reproduced here Fig. 2.87A). Two fragments of the holotype were examined for this study, one of which can be confidently located on the figure of the holotype by its substantial bifurcation (Fig. 2.87C). It can therefore be deduced that the exposed medulla is part of the main stem. The other fragment is a piece of branch or stem which cannot be reliably positioned on the figure of the holotype (Fig. 2.87B). Unfortunately, these two fragments are in a very poor condition with a single remaining partially attached polyp between them plus two detached polyp heads. Nevertheless, combining an examination of these fragments with Nutting's original description and the subsequent descriptions and figures of the holotype by Stiasny (1937) and Verseveldt (1942) it is possible to provide a reasonably complete re-description.

The original colony clearly had a main stem with a few short side branches, although they appear to be broken in places and the holdfast is missing (Fig. 2.87A). Nutting states that the main stem diameter is 3 mm and this is confirmed here. It appears from Nutting's figure that there are some anastomoses present in the colony, with possibly two loops identifiable. However, considering Nutting and Stiasny do not mention any anastomoses, and Verseveldt specifically says "there are no anastomoses" the colony loops are considered an artefact of the figure. According to Nutting there were six branches emanating from all sides of the stem and the calyces were arranged along those branches as well as the main stem. Nutting states that "the calyces are irregularly distributed on three sides of the proximal parts of the stem and branches and on all sides of the distal parts of the colony". However, Stiasny and Verseveldt both refute this, finding calyces and polyps on all sides throughout the colony. The fragments examined here have remnants of calyces spread evenly along and on all sides of the branches with up to 5 mm between them, although they are often closer than that (Fig. 2.87B, C).

In its original condition, the holotype had intact branch tips where, according to Nutting, the calyces "form definite clumps or clusters with the individual calyces averaging about 1.5 mm apart". There is a small clump present on one of the fragments examined here, with two or three calyces crowded together (Fig. 2.87C).

Colour:

Nutting mentions the colour as "very light yellowish brown". The holotype fragments are now cream in alcohol.

Calyces and polyps:

There are many calyces remaining on the holotype fragments but they are fragile and easily damaged with many of them already heavily impacted. Those in better condition are conical to cylindrical, usually 1–2 mm high and 1.5–2 mm wide, with a thin layer of sclerites arranged longitudinally to obliquely on their side walls (Fig. 2.87D). There is some tendency towards an *en chevron* arrangement of the calyx sclerites and Nutting states this is more pronounced around the calyx lip where the sclerites form "eight angular points around the margin". These points were not convincing on the fragments examined due to the damaged state of most of the calyces.

The single remaining polyp on the fragments is partially retracted such that the head rests on the calyx lip (Fig. 2.87E). It projects approximately 1.2 mm above the calyx and is 1.8 mm wide. Nutting states that most of the polyps are partly retracted like this and specifically that the "polyps are retractile". The polyp head is covered in sclerites arranged in a collaret and points and has sclerites which are particularly large and dense arranged along the back of the tentacles (Fig. 2.87E).

Medulla:

The medulla is made up of tightly packed, longitudinally arranged sclerites and is surrounded by an easily detached cortex approximately 0.2 mm thick (Fig. 2.88A). The medulla and cortex are separated by parallel, longitudinal canals which join and anastomose so as to form a boundary space with attachments between the cortex and medulla only occurring occasionally. In Verseveldt's paper (1942) he described the boundary canals in cross-section as "usually much flattened, on the cortex-side they are flat, on the medulla-side they are rounder. Their height in a radial direction amounts to 0.05–0.11 mm, sometimes to 0.16 mm; the breadth is 0.18–0.20 mm".

Additionally there is a cluster of 3 large, conspicuous coelenteric canals penetrating the centre of the medulla in the two fragments examined, with 2 or 3 other smaller and less distinct canals on the edge of the centre cluster (Fig. 2.88A). The larger canals range from 0.2–0.4 mm in diameter and do not appear to significantly differ in diameter throughout the two fragments examined.

For those polyps positioned along the branches, the polyp cavities terminate abruptly at the medulla with an almost flat base visible at the base of the calyx. Due to the scarcity of remaining material, the arrangement of the canals at the tip of the branches was not investigated. Verseveldt bemoaned his inability to thoroughly investigate the canal system of the holotype, particularly that near the terminal polyps, and finishes with "In my opinion it will depend on the behaviour of the medullary canals with regard to the terminal zooids, whether for *macrocalyx* quite a new genus must be assumed."

Sclerites:

Unfortunately the remaining polyp does not provide a good example of the arrangement of the sclerites on the polyp head with many sclerites dislodged and damaged. However, both Thomson & Dean (1931) and Verseveldt (1942) describe a ring of approximately 6–10 sclerites arranged transversely forming a collaret and similar sclerites arranged *en chevron* to longitudinally forming eight distinct points. These sclerites are mostly simple spiny-spindles with a relatively sparse covering of tubercles and range from 0.2–0.62 mm long (Fig. 2.88B). Mixed with these in the distal region of the points (and crossing over into the tentacle rachis) are large, clubbed, warty sclerites (Fig. 2.88C) arranged with their blunt clubbed ends towards the top of the points. Verseveldt specifically mentions that some sclerites from the points are "strong and club-shaped. I have not succeeded in finding the curious, thick and club-shaped spicules drawn by Thomson & Dean (1931, pl. XXIV fig. 6) and by Stiasny (1937, Textfig. Ja, b) anywhere either in cortex or medulla, they only occur in the anthocodiae." These club-shaped sclerites have sparse, distinctly projecting, conical tubercules with sharp, simple edges. Very few of these clubbed sclerites were sampled here but those examined were approximately 0.35–0.65 mm long. Verseveldt stated that "most of them are 0.50–0.65 mm long, but shorter ones also occur (0.30 mm); the club-shaped end is 0.085–0.120 mm thick, without processes."

Sclerites on the back of the tentacles are arranged longitudinally and are mostly short, fat rods with few, low tubercles (Fig. 2.89A, B). The larger, bulkier rods are white and opaque, and clearly visible on the back of the tentacles. Some of the rods are slightly clubbed with a clump of tubercles at one end of the sclerites, and they basically lie longitudinally with the tuberculate head placed towards the end of the tentacles. Sclerite length grades continuously from 0.17–0.40 mm with most of the bulky rods between 0.23–0.40 mm. The shorter sclerites are usually placed closer to the tip of the tentacles (Fig. 2.90A).

Many short, simple spiny-spindles and flat rods are crowded in the pinnules, all arranged longitudinally, and ranging from 0.04–0.23 mm long (Fig. 2.90A, B). There are only very sparse tubercules on these sclerites with a tendency for some of the sclerites to have very slightly clubbed or expanded tips, which always distad in the pinnules. There were no true josephinae clubs detected in the small sample available for examination. It may be that they are rare and were not sampled or it may be there are no josephinae clubs in the tentacles of this species.

No sclerites were detected in the pharynx.

The calyx has only a single layer of sclerites arranged in indistinct *en chevron* arrangements up the wall. These sclerites are all straight spiny-spindles with simple tubercles and thorns arranged haphazardly with no tendency for distinct asymmetry or clumping (Fig. 2.91). Length varies from 0.35–0.67 mm. Sclerites from the cortex are very similar (Fig. 2.92A). They are arranged longitudinally along the branch in a thin layer and are usually 0.35–0.67 mm long although some smaller sclerites are present. There are faint longitudinal corrugations in the cortex, presumably mapping the boundary canals below (Fig. 2.92B).

When magnified in transmitted light, most of the sclerites from the medulla are brown with a fibrous appearance. Similar to the calyx and surface, they are mostly straight spiny-spindles but many of them are smoother with very few tubercules (Fig. 2.93). There are also some with numerous tubercles (Fig. 2.93a) but these are not as common and there are some fused and branched sclerites. Length ranges from 0.27–0.90 mm although, as is often the case with medulla sclerites, the longer sclerites may be underrepresented due to breakage.

Sclerites are all transparent under transmitted light except the bulky sclerites in the tentacles and points and most medulla sclerites, which tend to be brown.

Distribution:

Indonesian archipelago

Depth:

1264–1165 metres.

Remarks:

The state of the holotype is such that any decisions on the status of this species must be made with some caution. It is clear this species should not stay in the genus *Anthothela* due to the colony growth form, presence of large coelenteric canals in the medulla and the lack of sclerites in the pharynx. All of these characteristics plus the general form and arrangement of the sclerites indicate a placement in *Victorgorgia.* The main caveat however, is the apparent absence of josephinae clubs in the tentacles. These particular sclerites are common in other *Victorgorgia* species so the lack of them in *V. macrocalyx* introduces a level of uncertainty to the reassignment. Given the limited material available for examination it is possible that the josephinae clubs are present but in small numbers and were simply missed during this necessarily limited analysis. The species is placed in *Victorgorgia* until new material can be examined.

This specimen is from deep waters off the coast of Indonesia. There has been very little sampling of this habitat and very little chance to amass more of this species. Additionally, the degree of connectivity of this area with other deep-sea areas is largely unknown thus the likelihood of recording this species in other places is, at this stage, unpredictable.

The presence of bulky, short rods on the back of the tentacles of *V. macrocalyx* is the main feature distinguishing this species from others in *Victorgorgia.* The most similar species is *V. alba* (=*A. nuttingi*) which has few josephinae clubs, similar thick rods on the tentacles and bulky clubs in the points. However, the rods from the tentacle rachis have more crowded, rounded tubercles than those from *V. macrocalyx.* Additionally, the large clubbed sclerites in the top of the points and base of the tentacles in *V. macrocalyx* have blunt, conical tubercles while the corresponding sclerites from the other species have crowded, rounded warts and tubercles. These differences are minor and subjective and both species descriptions are based on minimal material. It is possible that they are the same species but without further specimens from the type localities this is impossible to confirm.

V. josephinae and *V. argentea* have many josephinae clubs in the tentacles, *V. eminens* n. sp. lacks any large, bulky sclerites in the points or the tentacles and *V. nyahae* n. sp. has sharply tipped thorn clubs in the points and tentacles.

***Victorgorgia eminens* sp. nov.**

(Figs. 2.94–2.105)

Material examined:

Holotype: TMAG K4266, Z27 Seamount, Huon Commonwealth Marine Reserve (CMR), SW Tasman Sea, Australia, stn. J2-385-005, sample 010b, 44.245°S, 147.121°E, depth 1060 m, ROV JASON deployed from the U.S. RV *Thomas T. Thompson*, team led by Dr Jess Adkins & Dr Ron Thresher, 21st December 2008.

Paratypes: TMAG K4267, Z27 Seamount, Huon CMR, SW Tasman Sea, Australia, stn. J2-385-005, sample 10a, 44.245°S, 147.121°E, depth 1060 m, ROV JASON deployed from the U.S. RV *Thomas T. Thompson*, team led by Dr Jess Adkins & Dr Ron Thresher, 21st December 2008; **TMAG K4268,** Mongrel Seamount, Huon CMR, SW Tasman Sea, Australia, stn. J2-386-006, sample 001, 44.254°S, 147.115°E, depth 982 m, ROV JASON deployed from the U.S. RV *Thomas T. Thompson*, team led by Dr Jess Adkins & Dr Ron Thresher, 23rd December 2008; **TMAG K4269,** Mongrel Seamount, Huon CMR, SW Tasman Sea, Australia, stn. J2-386-011, sample 021, 44.255°S, 147.114°E, depth 899 m, ROV JASON deployed from the U.S. RV *Thomas T. Thompson*, team led by Dr Jess Adkins & Dr Ron Thresher, 23rd December 2008; **TMAG K4270,** Mongrel Seamount, Huon CMR, SW Tasman Sea, Australia, stn. J2-386-007, sample 003, 44.254°S, 147.114°E, depth 958 m, ROV JASON deployed from the U.S. RV *Thomas T. Thompson*, team led by Dr Jess Adkins & Dr Ron Thresher, 23rd

December 2008; **TMAG K4115,** Hill V Seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO RV *Southern Surveyor,* stn. 69,(SS199701/69), 44.397–44.398°S, 147.147–147.178°E, depth 1262–1854 m, 31st January 1997; **NTM CO13052 (ex TMAG K1360),** Hill J1 Seamount, SW Tasman Sea, Australia, CSIRO RV *Southern Surveyor,* stn. 36, (SS199701/36), 44.267–44.242°S, 147.332–147.363°E, depth 1518.4 m, 27th January 1997; **TMAG K4271,** E.N.E. of St. Patricks Head, eastern Tasmania, Australia, CSIRO RV *Soela,* stn. 16, (SO198705/16), 41.573 S, 148.743 E, depth 1090–1150 m, 9th May 1987.

Other material: NTM CO13050 (ex TMAG K1362), Dory Hill Seamount, SW Tasman Sea, Australia, CSIRO RV *Southern Surveyor,* stn. 47, (SS199701/47), 44.322–44.34°S, 147.115–147.072°E, depth 1280-1400 m, 29th January 1997.

Description:

Colony form:

The holotype is a large colony, about 230 mm high and 215 mm across, broken into two pieces, with an intact holdfast still attached to coral rubble (Fig. 2.94A, B). The irregular, relatively sparse branching is principally in one plane. Basally, there is a central stem, with an approximate diameter of 8.6 mm, from which narrower branches emanate with a few instances of anastomoses evident around the holdfast. Higher in the colony, the central stem becomes narrower with the diameter decreasing to 5.4 mm and side branch diameters between 3.4–5.3 mm in polyp-free areas. The branches are mostly circular in cross-section although tend to flatten at bifurcation points. Side branches occasionally branch again but are not crowded, with branches usually at least 15 mm apart. Anastomoses do not occur distally. The colony is in good condition although the tissues of the colony show evidence of dehydration from being frozen before being transferred to 70% alcohol. Calyces are placed irregularly around the branches, generally at right angles, occasionally bunched at points along the side branches and bunched tightly together on branch tips such that they form clavate clumps (Fig. 2.94C, D). Frequently, there are parts of the branches without calyces, up to 45 mm long on the main stem and 23 mm on the side branches. Occasionally there are isolated calyces, however more commonly they are crowded together in bunches with no or little space between them.

Colour:

In the in situ photographs by the ROV JASON, the colony is deep purple, however the freshly collected specimen, when photographed before preservation, was closer to magenta (Fig. 2.94B). The colony is now beige in alcohol.

Polyps and Calyces:

The calyces are distinct, compact and firm when the polyps are retracted. Many polyps are partially retracted such that the base of the polyp head sits on the lip of the calyx and other polyps are fully retracted within the calyx which form 2–3.5 mm high, conical mounds with a small, round aperture (Fig. 2.94D, E). The polyps and colony surface are covered with a thick, smooth skin which was partially removed to increase clarity in photographs (Fig. 2.94Da, b). Fully exsert polyps are rare but can be up to 3.5 mm tall, measured from the lip of the calyx, although they more commonly extend only 2.5 mm. Usually the tentacles are folded over the mouth to form an eight-lobed, rounded polyp head which at the widest point is approximately 3.2–4.2 mm across; some juvenile polyps had a head diameter of approximately 2 mm. There is a single row of 8–10 pinnules along each side of the tentacles.

Medulla:

The branches of the colony consist of an essentially cylindrical medulla of tightly packed longitudinal sclerites, surrounded by a thin cortex. Multiple adjoining longitudinal canals, which frequently anastomose to form a boundary space, separate the medulla from the cortex. The few points of attachment between the cortex and medulla make it easy to dislodge the cortex (Fig. 2.94F). Two or three large coelenteric canals (0.7–0.9 mm diameter in the main stalk, 0.3–0.4 mm diameter in the peripheral branches) penetrate the medulla longitudinally and appear to extend throughout the colony (Fig. 2.95A). Additional, smaller, indistinct canals occur adjacent to the larger canals in the medulla.

The gastric cavities of the polyps on the branches terminate at the medulla and are connected by solenia extending through the cortex and into the boundary space. The body cavities of the polyps at branch tips extend some way down the branch and appear to coalesce with the central medulla canals.

Sclerites:

Arrangements of the sclerites are largely obscured by the thick skin covering the colony. This skin was removed by a short immersion in bleach. The polyp heads are covered in tightly packed tuberculate sclerites, arranged to form a collaret and points (Fig. 2.95B). Transverse bunches of about 10 sclerites form the collaret at the base of the polyp head. These then grade *en chevron* up into the points, which continue longitudinally along the aboral side of the tentacles. The points and collaret sclerites are generally straight or curved, narrow spiny-spindles from 0.46–0.72 mm long which are sparsely covered in conical, flat-topped tubercules (Fig. 2.95C). Amongst these, occur smaller (0.11–0.29 mm), slightly flanged spindles with lateral, conical thorns (Fig. 2.95Ca). Below the polyp head similar long, straight or slightly curved tuberculate spiny-spindles are arranged obliquely and sparsely on the polyp neck. On retraction of the polyp, these sclerites become more transverse and crowded and grade into the collaret. Most polyps on the holotype are wholly or partially retracted so the polyp neck is rarely visible.

On the aboral side of the tentacles, sclerites are commonly straight josephinae clubs with simple tubercules, more crowded on and near the clubbed end and absent or only minor on the handle of the club (Fig. 2.96A). These sclerites are 0.18–0.30mm long, decreasing in length distad and are orientated with the clubbed end arranged towards the tentacle tip and bent upwards making the aboral surface of tentacles crowded and prickly (Fig. 2.96B). Crowded along the sides of the tentacle and projecting longitudinally into the pinnules are straight or bent-tipped josephinae clubs with particularly narrow, mostly smooth handles (Fig. 2.97), 0.2–0.37mm long. Also crowded longitudinally in the pinnules are shorter, lightly tuberculate spiny-spindles and flat rods, 0.01–0.29mm long (Fig. 2.97), some with slightly clubbed tips.

No sclerites were found in the pharynx.

In the calyx, sclerites are arranged obliquely to longitudinally but grade to transverse at the base. They do not appear to form chevrons or peaks as the sclerites are arranged haphazardly (Fig. 2.98A). They are mostly straight tuberculate spiny-spindles (Fig. 2.98B), usually between 0.3–0.53mm long, with sparse, conical tubercles. Shorter, almost smooth, narrow flanged spindles also commonly occur and range from 0.22–0.35mm long (Fig. 2.98Ba). Very rarely, sparsely tuberculated crosses occur (Fig. 2.98Bb).

The thin cortex commonly has straight tuberculate spiny-spindles (0.35–0.50mm long) (Fig. 2.99), arranged longitudinally and obliquely on the stem and branches along with much more complex tuberculated forms (Fig. 2.99a) that occur patchily in the cortex. In one particular sample they were more common that the tuberculate spiny-spindles but in other samples they were completely absent or rare. Most are between 0.14–0.35 mm long but some are up to 0.46 mm; they also tend to be wider than the smoother spiny-spindles. Occasionally shorter, mostly smooth, narrow flanged spindles similar to those from the calyx occur and, rarely, fused, cross or branched sclerites are present.

Tightly packed sclerites, mostly arranged longitudinally or obliquely, make up the medulla. These are mostly tuberculate or warty spiny-spindles, along with some almost smooth, narrow forms (Fig. 2.100). Fused sclerites are occasionally present. Sizes range from 0.45–0.90 mm long.

Sclerites are uniformly transparent and colourless under transmitted light.

Variation:

TMAG K4267 has a similar in situ colour to the holotype (Fig. 2.101A) and is from a site very close to that from which the holotype was collected, however there are a few differences in colony form and sclerite ornamentation. A number of anastomoses evident amongst the colony branches and a small membranous holdfast encrusting coral rubble with at least two attachment points for the colony mean the colony form is more contorted than the holotype (Fig. 2.101B). Sclerites from the tentacles are more complex than those from the holotype, particularly on the handles of the clubs (Fig. 2.101C) and the point sclerites are more tuberculate. The specimen also has calyx sclerites which are often broader than those from the holotype and tend to have a much more extensive cover of tubercules and sometimes complex warts (Fig. 2.101D). No substantially warty sclerites were observed from the cortex. Other specimens examined also have calyx sclerites with slightly more complex warts and tubercules but these sclerites have patchy distributions and are not always present.

Another colony collected from a different seamount but still within the same area (TMAG K4268), was deep purple in one in situ photograph but magenta under closer lighting, like the holotype (Fig. 2.102A, B). This colony has a branching pattern similar to the holotype, although not quite in one plane, with calyces clumped at branch tips and occasionally clumped along branches. However, in contrast to the holotype, calyces are also spread evenly and almost biserially, like *V. josephinae,* along the branches. Additionally, most polyps are fully exsert with almost none fully retracted, giving the preserved colony a slightly different appearance to that of the holotype.

Most of the other paratypes also have more exsert than retracted polyps giving the colonies a more untidy appearance than that of the holotype with its tightly retracted polyps. For example, K4271 is a large sample of many branched fragments (Fig. 2.102C). The colony branches are narrower and floppier than the holotype with some long branches having few or no secondary branching. Calyces are spread widely along branches and very clearly grouped at branch tips such that the branches curl over from the weight of the bunched polyps. Most polyps are exsert and bent over (Fig. 2.102D). A longitudinal cross-section of a terminal polyp bunch shows the extension of polyp body cavities down into the branch where they merge into the large coelenteric canals in the medulla (Fig. 2.102E).

Another specimen, NTM CO13050, is only tentatively included in this species due to differences in the ornamentation and shape of the sclerites. The colony is a similar colour to the holotype (Fig. 2.103A) but the polyps are larger and the calyces much more delicate than the holotype (Fig. 2.103B, C). The sclerites in the tentacles have a similar arrangement to the holotype—josephinae clubs in the sides of the tentacles and longitudinally in the pinnules and clubs arranged along the back of the tentacles (Figs. 2.103D; 2.104A). However, sclerites in the tentacles lack the bent tip present in those of the holotype. The smaller tentacle rachis sclerites particularly tend to be straight, tuberculate rods, not true josephinae clubs (Fig. 2.104Ba) while the large sclerites are clubs but more tuberculate than the holotype (Fig. 2.104Bb). Additionally, in general, all sclerites are more tuberculate than the holotype, including those from the pinnules, calyx and cortex (Fig. 2.105A–C).

Distribution:

Southern seamounts and east coast of Tasmania, Australia

Depth:

899–1854 metres.

Remarks:

V. josephinae has similar sclerite shapes and arrangements to *V. eminens* n. sp., however the most noticeable difference is the large josephinae clubs in the tentacles of *V. josephinae* in contrast to *V. eminens* n. sp. which has poorly developed josephinae clubs sometimes with slightly bent tips in the tentacles. Additionally, in *V. josephinae* the polyps tend to be arranged bi-serially while in this species there is a much greater tendency for the polyps to clump or bunch along and at the tip of the branches with notable regions of branches polyp-free.

Colour differences of the live colonies are striking—the colour of *V. josephinae* is recorded as “the coenenchyme ... was yellowish, while the anthocodiae were violet to deep purple” (López-González & Briand 2002) in contrast to *V. eminens* n. sp. which is uniformly magenta to deep purple. However, colour is not always a reliable species characteristic and is not helpful for determination after preservation. Geographic distance between the two specimens is similarly noteworthy (*V. josephinae* was collected off the coast of Portugal, *V. eminens* n. sp. off the coast of southern Australia).

The presence of large, dense, straight club sclerites in the points and aboral side of the tentacles of *Victorgorgia argentea* (Studer, 1894) distinguishes it from *V. eminens* n. sp. *V. alba* (=*A. nuttingi*) and *V. macrocalyx* both have bulky rods in the back of the tentacles and very few josephinae clubs and *V. nyahae* n. sp. has many sharply pointed thorn clubs along the back of the tentacles, in the points, and the calyx.

Etymology:

The epithet is the participle of the Latin *emino,* eminent or prominent, in recognition of the fact that the large, purple specimens are very obvious and distinct in photographs and video footage.

Victorgorgia nyahae sp. nov.

(Figs. 2.106–2.113)

Material examined:

Holotype: TMAG K3988, Cascade Seamount, Huon Commonwealth Marine Reserve (CMR), SW Tasman Sea, Australia, CSIRO RV *Southern Surveyor,* stn. 75, sample 32, (SS200702/075-032) 43.92–43.934°S, 150.463–150.479°E, depth 590–660 m, 10th April 2007.

Paratype: TMAG K3989, Cascade Seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO RV *Southern Surveyor*, stn. 77, sample 003, (SS200702/077-003), 43.915°S, 150.46°E, depth 590–660 m, 10th April 2007.

Description:

Colony form:

The holotype is a complete colony, now broken into three fragments (Fig. 2.106A). When whole, the colony had three main branches emanating from a small holdfast, encrusting a piece of coral rubble. The largest of these branches is approximately 29 mm in length with a diameter ranging between 1.8–2.9 mm and has a small group of polyps branching off close to the base. The other colony fragments are approximately 25–29 mm long with slightly narrower diameters (1.8–2.1 mm) and no secondary branching. The branches are occasionally bent and twisted, and often not circular in cross-section being more likely to be irregularly narrowed and distorted. No anastomoses are present. The colony holdfast is an encrusting membrane with a few scattered polyps. The colony is in good condition—preservation was directly into 70% alcohol.

Calyces and polyps are distributed along and all around the branches. They are particularly crowded towards the branch tip and so form terminal polyp bunches (Fig. 2.106B, C). All calyces and polyps project substantially from the colony, mostly at right angles to the branches, with large, prominent calyces and rounded polyp heads. There is little space between calyces and only a few are isolated.

Colour:

The photograph taken soon after collection shows the polyps and the distal half of the calyces are lilac, the retracted tentacles are purple and the rest of the colony is light cream. The colony is now light beige in alcohol.

Calyces and polyps:

The straight-sided calyces are large relative to the branch diameter and range from 2.4–3.9 mm tall and 1.4–2.6 mm wide. There are no polyps with the head fully retracted into the calyx although some are slightly retracted such that the polyp head is sitting on the lip of the calyx. Occasionally a partially retracted polyp head causes the calyx lip to flare out while the polyp head flattens (Fig. 2.106Ca) making the whole polyp and calyx quite short and squat, however the majority of the polyps are exsert. Exsert polyps extended between 2–2.8 mm above the lip of the calyx and the polyp heads have diameters of approximately 2–2.75mm (Fig. 2.106D). Both polyps and calyces are covered in a dense layer of crowded sclerites. Most polyps have the tentacles tightly folded over the polyp mouth so the polyp heads are rounded mounds with eight segments (Fig. 2.107A). There are approximately 8–10 pinnules arranged in a single row along each side of the tentacles.

Medulla:

The branches of the scleraxonian colony are composed of a central medulla, made up of tightly packed longitudinal sclerites, surrounded by a thin cortex. The cortex and medulla are separated by a crowded series of longitudinal canals which anastomose to form an encircling boundary space allowing the cortex to be easily separated from the medulla. At the breakage point of the largest piece of colony, it can be seen that the medulla is extensively penetrated by longitudinal canals (Fig. 2.107B, C). Many are large and encircled by a thin transparent layer of mesogloeas, as mentioned by Lopez-Gonzalez and Briand, 2002 for *V. josephinae*. However, not all the canals have this layer and many are small and indistinct. For polyps which are arranged along and perpendicular to the branches, gastric cavities terminate at the medulla. For polyps which form the polyp clumps at the branch tip, their body cavity can extend internally down the branch for a short distance eventually merging into the coelenteric canals in the central medulla.

Sclerites:

The polyps and calyces are strongly protected with a dense covering of sclerites, predominately tuberculate spiny-spindles. On the polyp head sclerites are arranged as a collaret and eight spiky points, with the sclerites bunched and crowded (Figs. 2.106D; 2.107A). Around the head, approximately 10–15 transverse rows of sclerites form the collaret. Sclerites then angle *en chevron* up into the points, and eventually are longitudinally arranged at the tip of the points where the back of the tentacles begin. The collaret and point sclerites are mostly composed of tuberculate or warty spiny-spindles slightly curved or straight (Fig. 2.108). The points also have protruding, often large, warty spindles and clubs which are arranged with modified spear-tips sticking out from the polyp head at the top of the points (Figs. 2.107A; 2.108a). These sclerites give the polyp head a distinctive spiky appearance. Simple sclerites from the points and collaret range from 0.32–0.65 mm long while the more complex sclerites usually range from 0.5–0.7 mm long with occasional longer sclerites up to 0.91 mm. The sclerites from the polyp neck are simple tuberculate spiny-spindles, arranged obliquely, becoming transverse in the slightly contracted polyps.

Sclerites continue longitudinally along the aboral side of the tentacles from the points (Fig. 2.109A). These sclerites are sharply pointed thorn clubs with a tuberculate handle and an often bent, foliose or thorny tip (Fig. 2.109B). The thorny tip of the sclerites is distad in the tentacle and the bent tips project up from the back of the tentacle making it very bristly. The sclerites decrease in size distally along the tentacle rachis, grading from approximately 0.5 to 0.18 mm. Amongst these thorn clubs are josephinae clubs (Fig. 2.110) with long, mostly smooth handles and rounded spiny bent tips. They tend to occur along the sides of the tentacles and extend into the pinnules with the thorn clubs mostly restricted to the middle proximal ridge of the rachis (Fig. 2.109A).

Sclerites, 0.1–0.27 mm long, are crowded longitudinally in the pinnules, reaching approximately half way down. They are mostly sparsely tuberculate, flat rods, straight clubs and josephinae clubs with the clubbed tips pointing distad (Fig. 2.110). Some of the larger sclerites have a reasonably well-developed clubbed tip, blurring the distinction between pinnule and tentacle rachis sclerites. There are also very small, flat rods with jagged edges and without clubbed ends (Fig. 2.110a)—these appear to crowd around the distal end of the tentacle and can appear to be arranged transversely although this may simply be an artefact of contraction of the tentacles (Fig. 2.109A).

Calyces are covered in tightly packed sclerites, almost all spiny-spindles with tubercles varying from simple to complex branched warts (Fig. 2.111). Sclerites can range from 0.13–0.88 mm long but most are between approximately 0.36–0.78 mm. Bulky spindles with complex warts can have a thorny tip (Fig. 2.111a) although these are not as developed as those present in the points and tentacles. Most sclerites are positioned longitudinally on the calyx, and tend to group into columns so the calyx has eight vaguely defined longitudinal ridges ending a the lip as eight indistinct mounds. The warty spindles are all orientated with the thorny tip projecting out from the calyx sometimes giving the calyx a slightly prickly appearance particularly near the lip. A few small, almost smooth, flanged spindles can also be found (Fig. 2.111b).

No sclerites were found in the pharynx.

The thin cortex of the colony is composed of a dense layer of longitudinally arranged spiny-spindles from 0.23–0.71 mm long (Fig. 2.112). Most sclerites have mainly simple tubercules and conical thorns but there are some spindles with a dense covering of complex warts. Additionally, small flanged spindles (0.12–0.19 mm long) occur randomly distributed among the large sclerites (Fig. 2.112a).

The medulla is composed of tightly packed longitudinal sclerites—mostly tuberculate and warty spiny-spindles (Fig. 2.113). Occasionally there are large spiny-spindles with only sparse warts, often with branches, forks and fused areas. Bulky spindles with complex warts are also present but only

infrequently. Most sclerites are from 0.30–0.76 mm long although longer sclerites were observed (up to 1 mm). It was difficult to ensure these long sclerites remained undamaged during sampling so the prevalence of these cannot be estimated. Similar to the calyx and surface, small flanged spindles, from 0.12–0.22 mm in length, occur amongst the bigger sclerites.
Sclerites are uniformly transparent under transmitted light.

Variability:

The paratype is a small fragment closely resembling the holotype. It is a piece of a narrow branch with polyps which have a similarly prickly appearance, obvious large, straight-sided calyces and polyps which are mostly extended. No polyps are fully retracted. The sclerites are similar to those in the holotype. Unfortunately there is no live photograph of this colony.

Distribution:

Southern Tasmanian seamounts

Depth:

590–660 metres.

Remarks:

V. nyahae n. sp. is differentiated from other *Victorgorgia* species by the presence of sharply pointed thorn clubs and spear-tipped spindles in the tentacles, points and top of the calyx. See Section 2.3.3 for details of the divergent sequences obtained from the two specimens.

Etymology:

The species is named after Nyah Inglis, my daughter, as a small recompense for a childhood overshadowed by my PhD thesis.

***Williamsius* gen. nov.**

Diagnosis:

Monomorphic scleraxonians which form arborescent colonies with a single, short main stem; simple, sparse branching basically in one plane; anastomoses absent; medulla without large, well-defined coelenteric canals, separated from the cortex by a ring of boundary canals; polyps sparse, retractile into tall calyces on all sides of branches but restricted to the distal half of the branches; sclerites predominately short, flat rods arranged transversely in the tentacle rachis, transverse scales in pinnules, small tuberculate rods from the neck and pharynx, and tuberculate spiny-spindles in the points, calyx, cortex and medulla.

Type species: *Anthothela parviflora* Thomson, 1916 here designated.

Etymology:

This genus is named in honour of Dr Gary Williams in recognition of the extensive research conducted by him on octocorals from the waters around South Africa, including a redescription of the type species of the genus.

Williamsius parviflora **(Thomson, 1916) new combination**

(Figs. 2.114–2.121)

Anthothela parviflora Thomson, 1916: 3–6, Pl. II Fig. 5, Pl. V Fig. 4; Williams 1992, Figs. 2–3, 4A–D.

M**aterial examined**:

Paralectotype: three fragments of **NHMUK 1962.7.20.40**, off Algoa Bay, South Africa, 'P.F. 524', depth 183 m, 1st November 1898, S.J. Hickson collection.

Description:

Colony form:

The fragments examined here are from one of three syntypes which was only briefly mentioned in Thomson's (1916) original description. His description was based on the "most complete example" which was probably the specimen designated as the lectotype by Williams (1992a). Unfortunately it was not possible to view the lectotype which is stored at the South African Museum. The material examined here is from a different location to the lectotype but corresponds with Thomson's extensive description and strongly resembles the figures in Williams (1992a).

The complete lot consists of a small, incomplete colony plus the three fragments examined here (Fig. 2.114A). They are all pieces of branches with tall calyces emanating at right angles or obliquely from the branch (Fig. 2.114B). The largest fragment is 51.5 mm long with eleven polyps spread evenly along it, another fragment is 28 mm long with seven visible polyps (approximately half of the branch is surrounded by an encrusting sponge) and the smallest fragment is 14 mm long with four polyps. The two smallest pieces have intact branch tips which have small clumps of adult polyps (one has two juvenile polyps on the very apex of the branch). None of the fragments examined have any evidence of branching, however the largest portion of the colony pictured in Fig. 2.114A is consistent with the species description by Thomson; that is, colonies with a spreading base, sparse, irregular branching, basically in one plane, bifurcation at approximately 45 degrees and branches which are twisted or curved. There are no anastomoses noted for the three specimens described by Thomson (1916) or the four colonies examined by Williams (1992a), although Thomson does mention that colonies can be “creeping”, perhaps indicating this species can grow both membranous and branching forms. Williams, however, does not mention any such growth form from the four “whole” colonies included in his description.

The three branch fragments are circular in cross-section and diameter varies little (from 1–2 mm). In the larger colony portion pictured, the major branches are up to 3 mm wide while the bulky basal stem is approximately 5 mm wide.

All fragments are in good condition with mostly intact polyps and an undamaged colony surface.

Colour:

No mention is made of live colour by either Thomson or Williams, although Thomson mentions that the (presumably preserved) colony has a “slightly silvery appearance”. This is more likely due to the dense layer of sclerites than colony colour. The fragments are now cream in alcohol.

Polyps and calyces:

Calyces are sparsely arranged on all sides of the branches, approximately 3.5–5 mm apart. Terminal clumps of calyces are not large or overly crowded (Fig. 2.114C). The calyces are tall and cylindrical, with eight distinct longitudinal furrows. Most calyces are approximately 3–4.5 mm tall and 1.5–2.0 mm wide although there are rare calyces only 2–2.5 mm tall. The exsert part of the polyps are approximately 1–2.3 mm tall but none are fully extended—most have the polyp head resting on the lip of the calyx (Fig. 2.114D). Polyp heads are approximately 1.3–1.6 mm in diameter and some are fully retracted into the calyx (Fig. 2.115A). The tentacles are often crumpled in a haphazard way over the polyp mouth (Fig. 2.115B), although there are occasionally polyps with the tentacles folded in, across the polyp mouth, giving those polyps a mounded, starred apex to the polyp head. There is a single row of 10 very long and narrow pinnules along each side of the tentacles. The pinnules taper to a sharp tip and often twist and curl.

Medulla:

The medulla is constructed of tightly packed sclerites, arranged longitudinally in general, and is surrounded by a cortex, similarly consisting of crowded sclerites. The cortex is distinctly separated from the medulla by a ring of relatively large and well-defined boundary canals (Fig. 2.116A). These canals do not obviously anastomose to form a boundary space but run longitudinally, adjacent to each other, the length of the fragments. This is similar to that seen in specimens of *Anthothela* although here the canals are much larger relative to the diameter of the branches; within the 1–2 mm branch diameter the boundary canals have approximate diameters of 0.1–0.15 mm. The cortex is approximately 0.1–0.2 mm thick while the medulla is approximately 1-1.5 mm in diameter. There are no coelenteric canals within the medulla. Thomson (1916) mentions “a few small canals” in the medulla but there was no indication of such found here.

Due to the scarcity of material, no investigation was conducted on the canal arrangement at the branch tips.

Sclerites:

Sclerites cover the calyces and polyps. On the polyp head, straight or very slightly curved, tuberculate spiny-spindles are arranged in eight points (Fig. 2.116B, C). These sclerites are 0.18–0.38 mm long and are arranged longitudinally on the central ridge of the points, and *en chevron* to obliquely on the sides of the points. A collaret is not present. There are intermediate sclerites arranged longitudinally between the points, with clumps of up to five sclerites proximally, reducing to only one or two sclerites distally (Fig. 2.116Ba). They are similar in form to the sclerites of the points. In the distal part of the points, the longitudinally arranged spiny-spindles cease and are replaced by transversely arranged, small, lightly tuberculate, mostly flat rods (Fig. 2.117A, B) along the back and side of the rachis. They continue to the tip of the tentacle, decreasing in size distad and range from 0.11–0.21 mm in length. The pinnules have numerous small, very lightly tuberculated scales (Fig. 2.117C). Some are bow-shaped or have a waist but most or straight with slightly crenulated edges. They are arranged transversely in the pinnules (Fig. 2.117A), and although numerous, are not overly crowded. Their length ranges from 0.05–0.12 mm.

The polyps have an irregular arrangement of sclerites spread over the neck region, mostly short rods with simple tubercules (Fig. 2.118A). Sizes range from 0.07–0.19 mm long.

The pharynx is fleshy and thick, and when contracted shows rounded, transverse ridges which are possible muscle bands (Fig. 2.118B). Sclerites are rare or absent proximally but distally are arranged in indistinct longitudinal groups. These differ slightly from the common form for pharynx sclerites and are short rods with few tubercules (Fig. 2.118C), similar to those in the neck. They are approximately 0.08–0.13 mm long.

On the calyces, the sclerites are arranged mostly longitudinally or slightly obliquely and are quite crowded together. They are visible as a silvery layer with individual, large sclerites discernible for most of the calyx but at the lip smaller sclerites overlap so only the tips of sclerites are visible (Fig. 2.116B). Almost all are narrow to stout spindles with simple to relatively crowded tubercles (Fig.

2.119) and they range from 0.1–0.32 mm long. The smallest sclerites are flanged spindles (0.06-0.1 mm long) (Fig. 2.119a).

In the cortex, the sclerites are similar to those from calyx, that is, spiny-spindles with simple tubercules through to complex warts (Fig. 2.120) and they are 0.06–0.34 mm long. There tends to be a higher percentage of warty spindles, particularly short, stout ones (Fig. 2.120b), in the surface than in the calyx but this may be an artefact of sampling or patchiness. Small flanged sclerites are also present (Fig. 2.120a).

The medulla contains the same kind of warty spindles as found in the cortex as well as simple, lightly tuberculate spiny-spindles, short flanged spindles and rare warty crosses (Fig. 2.121). The tuberculate spiny-spindles are easily damaged or broken during the sampling process so maximum length is an underestimate, but they appear to be 0.11–0.4 mm long. The warty spindles are relatively consistent in length (0.18–0.25 mm) while the flanged spindles are only 0.06–0.1 mm long. All sclerites are universally transparent and colourless under transmitted light.

Distribution:

This species has rarely been reported and it is assumed it is restricted to the waters around South Africa (G. C. Williams 1992b). Considering the report by Williams (1992a) on four full colonies in one trawl in an area outside the type locality, the species may be locally common.

Depth:

180–500 metres.

Remarks:

This species was originally placed in the genus *Anthothela* by Thomson on the then justifiable grounds of a similar scleraxonian medulla and mostly comparable polyp and sclerite form. Based on the re-definition of *Anthothela* herein, this species can no longer be considered an example of the genus due to the distinct differences in the sclerites of the tentacles and pinnules and in the colony form. *Anthothela* species have tuberculate spiny-spindles arranged longitudinally along the rachis of the tentacle, while *W. parviflora* n. comb. has short, flat rods arranged transversely along the tentacle. Similarly *Anthothela* species have long, narrow-handled spatulate clubs crowded longitudinally in the pinnules where *W. parviflora* n. comb. has short scales arranged transversely. Differences in colony form are also noteworthy—specimens of *Anthothela* have no single trunk or main stem, having instead a tangled, anastomosing colony form with little consistent structure and crowded polyps, while specimens of *W. parviflora* have single trunks with no noted examples of anastomoses and only sparse branching and relatively isolated polyps.

A potential complication should be noted in that, in his discussion comparing his new species with *Anthothela grandiflora,* Thomson (1916) mentioned that *A. parviflora* has “long, thin spindles or rods with few processes” in the tentacles and that these are similar to those found in *A. grandiflora* “but apparently in some cases at least are much longer”. This description does not correspond to the short, flat transverse rods found in the tentacles in this study. One possible explanation for this is a difference between the lectotype (which Thomson described) and the paralectotype (described here). Alternatively, and perhaps more likely, Thomson was erroneously referring to the sclerites from the points. In his re-description of the species where the lectotype was designated, Williams (1992a) does not document the placement of sclerites on the polyp, mentioning only that there are “numerous needle-like spindles or a few stout rods”. Without further investigation of the lectotype some uncertainty remains but unfortunately requests to the South African Museum were unanswered. Regardless, the paralectotype investigated here cannot remain within the genus *Anthothela* and on the assumption that the lectotype and the fragments described above represent the same taxon, the species is re-assigned.

The combination of a sparsely branching, arborescent colony with no coelenteric canals in the central medulla, widely dispersed, tall calyces, short, flat, transverse rods and scales in the tentacles and a predominance of broad, warty spindles in the calyx distinguishes this colony from all other genera in the family Anthothelidae.

***Lateothela* gen. nov.**

Diagnosis:

Monomorphic scleraxonians which form bulky, complex colonies; often with an extensive membranous or encrusting growth, from which multiple, upright, robust branches emanate; some secondary branching occurs; anastomoses present; medulla without well-defined coelenteric canals; ring of boundary canals encircling medulla, clearly defining the cortex; distinct, robust calyces with a smooth mat-like surface; sclerites include tuberculate spiny-spindles, rodlets and spiky clubs; preponderance of short, stout warty rodlets in calyces and surface; tentacles rachis has longitudinally arranged tuberculate spiny-spindles and spiky clubs; pinnules crowded with longitudinally arranged spiky josephinae clubs.

Remarks:

Within the family, the other comparable genera are *Anthothela, Victorgorgia* and *Briareopsis* Bayer, 1993. Specimens of *Lateothela* n. gen. have been mistakenly identified as *Anthothela grandiflora* for over 150 years. Superficially the colonies are similar with a complex construction of both encrusting and branched forms, similar colour and habitat and comparable calyces and polyps.

The main features of *Lateothela* n. gen. which differ from those of *Anthothela* are:

1. Preponderance of short, stout, warty rodlets in the cortex and calyx (*Anthothela* specimens chiefly have tuberculate spiny-spindles).
2. Many spiky josephinae clubs in pinnules and tentacle rachis, few or no flat spatulate clubs (*Anthothela* specimens have many spatulate clubs and few or no josephinae clubs).
3. Crowded mixed sclerite forms on the polyp neck including spiky clubs (*Anthothela* specimens have only sparse tuberculate spiny-spindles on the polyp neck).
4. Colony robust, with a tendency for multiple branches to grow roughly perpendicular from a membrane with only minor secondary branching or anastomosing (*Anthothela* specimens have many narrow, tangled, commonly anastomosing branches growing without any discernable organization).

The main features of *Lateothela* n. gen. which differ from those of *Victorgorgia* are:

1. Spiky headed josephinae clubs in the tentacles (*Victorgorgia* has josephinae clubs which lack spikes with small, rounded tubercles only).
2. No central coelenteric canals in the medulla (*Victorgorgia* has clearly defined central coelenteric canals in the medulla).
3. Colony robust, with a tendency for multiple branches to grow roughly perpendicular from a membrane with only minor secondary branching or anastomosing (*Victorgorgia* has arborescent colonies).

Lateothela n. gen. should be compared to *Briareopsis* due to a similarity of sclerites but *Briareopsis* has a distinct single main stem which then branches dichotomously, the cortex is divided into two layers (the inner layer is very spongy), the medulla and cortex are only poorly differentiated by boundary canals and the polyps retract into very low calyces (Bayer 1993).

Lateothela n. gen. actually appears to be relatively common in the northern eastern Atlantic, especially around Norway and in the north western Atlantic along the North American continental shelf (Scott France, pers. comm.) and can form large and extensive colonies, however its true identity has remained overlooked due to the erroneous assumption it was *A. grandiflora.* There is a possibility that specimens from this genus have been collected as membranous colonies only, presumably prior to the formation of branches, and thus not associated with the scleraxonia. In Stokvis & van Ofwegen (2006) three species of *Alcyonium* are figured which are all membranous but otherwise have distinct similarities to sclerites from *Lateothela* n. gen. In particular, the specimen determined as *Alcyonium grandiflorum* has spiky josephinae clubs in the pinnules and tentacles as well as the short, stout, tuberculate rods and short clubs in the calyx and cortex. Similarly, *A. profunda* and *A. rubrum* in the same publication have comparable sclerites to *Lateothela* n. gen. The relationship of *Lateothela* n. gen. with nominal *Alcyonium* species, using both morphological and molecular characters, (see section 2.3.3) is intricately entwined and worthy of further investigation.

Type species:

Lateothela anitorkilda n. gen., n. sp. by designation and monotypy.

Etymology:

The new generic name is derived from the Latin, *lateo* (to lurk, lie hidden or escape notice) and *thela* in recognition that the genus has long been mistaken for specimens of *Anthothela*.

Lateothela anitorkilda sp. nov.

(Figs. 2.122–2.139)

Anthothela grandiflora Broch 1912b (?part): 5–9, Figs. 1–3; Molander 1918 (?part): 6–8, Fig. 1; Kükenthal 1919 (?part): 17, 19, 26, 43–44, 672, 681–685, 730, 788, 796, Figs. 17, 315; Verrill 1922 (?part): 18–19, Fig. 2, Pl. VI Figs. 1–4; Kükenthal 1924 (?part): 14–16, Figs. 13–14; Stiasny 1937 (?part): 20–23, Figs. F^1, F^2, Pl. I Figs. 6, 7; Verseveldt 1940 (?part): 37–47, Figs. 13–15; Carlgren 1945 (?part): 33–34, Fig. 8; Grasshoff 1981 (?part): 745, Karte 1, 942.

Material examined:

Holotype: NTNU-VM 63143, Rødberg, Trondheimsfjord, Norway, 63.468°N, 10.0°E, depth 200–300 m, 5th December 2006.

Paratypes: NTNU-VM 68106, Agdenesflua, Trondheimsfjord, Norway, 63.656°N, 9.766°E, depth 202–291 m, 12th June 2012; **NTNU-VM 67147,** Agdenesflua, Trondheimsfjord, Norway, 63.656°N, 9.766°E, depth 150–50 m, 30th June 2011; **NTNU-VM 63140,** Agdenesflua, Trondheimsfjord, Norway, 63.651°N, 9.763°E, depth 84–147 m, 1st July 2008; **NTNU-VM 40341 (part)**, Dyrviknes 27, Trondheimsfjord, Norway, 63.603°N, 9.757°E, depth 120 m, 18th May 1965; **NTNU-VM 40336,** Trondheimsfjord, Norway, determined by Broch as *Anthothela grandiflora,* depth and date unknown; **NTNU-VM 39877,** Rødberg, Trondheimsfjord, Norway, depth 400–500 m, 9th September 1911; **ZMUB unregistered,** Norway, Zoological Museum of Bergen, collected by Håkon Mosby-Møre, stn. 1, 10th October 2005; **ZMUB 60246,** Handangerfjord, Norway, determined by A. Fosshagen as *Trachymuricea kukenthali,* 59.813°N, 5.586°E, depth 180–260 m, 6th June 1959; **ZMUB 17759 (part),** Skarnsundet, Trondheimsfjord, Norway, determined by Storm as *Anthothela grandiflora,* depth unknown, August 1899; **ZMUB 12120,** Totlandsholmen, Bryggen, Nordfjord, Norway, determined by Grieg as *Anthothela grandiflora,* depth 450 m, July 1899; **ZMUB 3897,** Rødberg, Trondheimsfjord, Norway, depth and date unknown; **ZMUB 548,** Flora, Batalden, Norway, depth and date unknown; **NHM,UIOslo B1367,** Rødberg, Trondheimsfjord, Norway, determined by Jungerson as *Anthothela grandiflora,* depth and date unknown; **NHM,UIOslo B1368,** Between Rūltetangen and Solsvik, Norway, depth 400–500 m, 21st October 1949; **ZMUC-ANT-000467,** Rødberg, Trondheimsfjord, Norway, determined by Mortensen as *Anthothela grandiflora,* depth 300 m, 27th July 1911; **ZMUC-ANT-000468,** Trondheimsfjord, Norway, determined by Jungersen as *Anthothela grandiflora,* depth unknown, 27th April 1887; **ZMB 5527 (part),** Rødberg, determined as *Anthothela grandiflora* by Broch, Trondheimsfjord, Norway, depth 300–350 m, 1913; **ZMB 5847,** Skarnsund, Trondhjemsfjord, Norway, Scholtlaener Expedition 1911, depth 150–240 m, 1911; **ZMB 2686,** Trondheimsfjord, Norway, depth 180 m, 1886; **ZMB 2545,** Trondheimsfjord, Norway, depth unknown, 1881; **NHMUK 1962.7.20.210,** Trondheimsfjord, Norway, H. Graham Cannon, depth and date unknown; **NHMUK 1898.5.5.38,** Rødberg, Trondheimsfjord, Norway, Norman Collection, depth 457 m, date unknown; **NHMUK 1917.6.7.1,** Pernambuco Plateau, east coast of Brazil, determined as *Stereogorgia claviformis*, 7.617°S, 34.433°W, depth 274 m, date unknown.

Other material: USNM 1139021, West Florida slope, Gulf of Mexico, USA, USGS Discovre GOM 2009, Lophelia II, DSRV Johnson Sea Link II, RV Seward Johnson, 26.204°N, 84.727°W, depth 498 m, 16th September 2009; **TMAG K4272**, Gulf of Mexico, USA, Lophelia II, stn. 276 (LII-09-276), 28.441°N, 89.318°W, depth 541 m, 10th September 2009; **USNM 1207952**, Gulf of Mexico, USA, Lophelia II, LII-10-312, 29.166°N, 88.017°W, depth 489 m, 22nd September 2010; **USNM 1207953**, Gulf of Mexico, USA, Lophelia II, LII-10-352, 26.336°N, 84.756°W, 507 m, 1st October 2010.

Description:

Colony form:

The holotype consists of seven fragments of what was probably one colony (Fig. 2.122A). The main holdfast is an encrusting, membranous part of the colony, growing over coral rubble. From this encrusting part, five branches emanate basically perpendicular to the membrane and roughly parallel to each other. There are examples of anastomoses, predominantly at the bases of the branches. These upright branches are slightly flexible, but will snap if bent, are reasonably robust, a relatively consistent diameter (4–6.4 mm) and range from 46–83 mm long. One cluster of polyps exists on the tip of a very short (17.8 mm), narrow branch (2.2 mm diameter) (Fig. 2.122Aa). Occasionally, the upright branches have secondary branching but only close to the distal end and any secondary branches are quite short, ranging from 3.3–4.6 mm only. In general, the branches range between oval to circular in cross-section but at places where polyps occur and at points of bifurcation the branches can be distorted.

Calyces and polyps are distributed throughout the colony, on all sides of the branches and also on the membranous part. There is a tendency for the calyces to crowd together in terminal bunches (Fig. 2.122B). The largest distance where there are no calyces is only approximately 5 mm with most closer together.

The colony, although in a number of fragments, is in good condition with many intact polyps and much unbroken colony surface.

Colour:

There is no photograph or record of the live colour of the holotype but the paratype NTNU-VM 67147 was creamy peach to light apricot whilst alive (Fig. 2.122C) and other paratypes have been described as “peach” and “rose pink”. The holotype is now light cream in alcohol.

Polyps and calyces:

Calyces are relatively short, flat-topped, conical projections which protrude, in general, at right angles to the branches except at branch tips where they crowd together at many angles (Figs. 2.122B; 2.123A). They range from 1.5–2.5 mm tall and 2.5–3.8 mm wide. All are covered with a layer of tightly packed sclerites giving a very smooth appearance. Some of the calyces have eight minor bulges or longitudinal ridges at the lip of the calyx corresponding to the eight points on the polyp head. The majority of polyps are partly retracted or invaginated such that the base of the polyp head sits on the lip of the calyx or the polyp head is partly enclosed in the calyx (Fig. 2.123B). There are examples of entirely retracted polyps with the calyx closed over the top of the polyp head and rare examples of partially extended polyps where the polyp neck area is visible which can be slightly swollen or ballooned out above the firm calyx (Fig. 2.123C, D). The exsert part of the polyps can be 3–5 mm tall but most commonly just the polyp head is visible, approximately 2–2.5 mm tall. Polyp heads are approximately 2–3 mm across at the widest point. Occasionally juvenile polyps occur; these are approximately 0.8–1.3 mm tall and 1.3–1.5 mm wide. All polyps have the tentacles neatly and tightly closed within the mouth giving the polyps a consistent starred appearance with eight rounded mounds. There is a single row of 8–10 very fleshy pinnules arranged along each side of the tentacles, some of which extend around the tip.

Medulla:

The upright branches have a medulla composed of tightly-packed, longitudinally or obliquely arranged sclerites surrounded by a thin cortex. There are many small canals between the medulla and cortex running longitudinally throughout the colony creating a distinct boundary between the medulla and the cortex. They are clearly defined, adjacent canals which do not anastomose (Fig.

2.124A). There are no obvious coelenteric canals within the medulla, either at the base of the branches or at the tips. Small solenia penetrate the medulla and cortex, facilitating connections between the polyps and the main boundary canals.

Along the branches, polyp body cavities truncate evenly at the medulla while in the terminal bunches, polyp body cavities extend only slightly within the branches, merging into the boundary canals.

Sclerites:

The calyces, polyps and colony surface are all covered in sclerites. The heads of the polyps are coated in a crowded layer of sclerites, which are arranged *en chevron* at the base and sides of the points and longitudinal at the base of the tentacles (Fig. 2.123C). They are mostly straight to slightly curved spindles with a light to moderate covering of simple, often tall, tubercles (Fig. 2.124B). Occasionally, smaller sclerites with a tendency for one tip to be clubbed or more tuberculate were noted but they are not common (Fig. 2.124Ba). Lengths range from 0.19–0.65 mm but most are between 0.2–0.6 mm long. Immediately basal to the points, similar sclerites are arranged transversely to obliquely and form a diffuse collaret when the polyp is retracted.

From the tip of the points, the crowded sclerites continue longitudinally along the back of the tentacles (Fig. 2.125). There are a mixture of forms: small clubs with flame-like spikes on the head (0.09–0.25 mm long) (Fig. 2.126a); mostly straight, lightly tuberculate spiny-spindles (0.2–0.48 mm long) (Fig. 2.126b) and short, straight, sparsely tuberculate flat rods (0.1–0.2 mm long) (Fig. 2.126c). Most sclerites are arranged longitudinally along the back of the tentacle with any clubbed or spiny tips always arranged distad, although in the distal quarter of the tentacle the flat rods sometimes appear to lie transversely. The small clubbed sclerites (Fig. 2.126a) are arranged in a thin upper layer along the centre of the tentacle rachis (Fig. 2.125) with the other types of sclerites forming the lower layers and on sides of the tentacles. Sclerite length tends to decrease distally.

The pinnules are fleshy and relatively large with narrow sclerites crowded longitudinally (Fig. 2.125). However, this fleshy nature combined with few sclerites actually reaching the distal tip of the pinnules means it is possible to conclude, erroneously, that there are no sclerites in the pinnules. The sclerites include narrow, tuberculate spiny-spindles (0.1–0.26 mm long) and narrow, spiky, josephinae clubs with rounded, bent heads with flame-like spines (0.2–0.4 mm long) (Fig. 2.127). Some of the spiky josephinae clubs are found along the sides of the tentacles, extending into the top of the pinnules.

Below the polyp head and diffuse collaret, the polyp neck is covered in a crowded layer of haphazardly arranged sclerites (Fig. 2.123C, D). The majority of the neck sclerites are short, straight, tuberculate spiny-spindles and clubs and some warty rodlets with a dense covering of tubercules

(Fig. 2.128A). There are also occasionally small, tuberculate crosses, some of which are unevenly developed and some longer, simple, straight, tuberculate spiny-spindles, resembling those from the points (Fig. 2.128A). Lengths range from 0.2–0.45 mm for the spiny-spindles to 0.08–0.22 mm long for the small rodlets and clubs and the crosses are approximately 0.07–0.11 mm.

Numerous small spiny-spindles and rods with simple tubercles are found in the pharynx (Fig. 2.128B). These are a relatively uniform size, with most only ranging from 0.09–0.15 mm long, although there are occasionally longer sclerites, up to 0.2 mm long. Small crosses are also occasionally found.

Calyces are covered in a dense, smooth layer of sclerites which are small enough to knit together to commonly create a mat-like appearance to the surface (Fig. 2.123A, B) and it is difficult to see individual sclerites through a dissecting microscope. There are many short, thick, warty rodlets with a dense covering of tubercles; tuberculate clubs; and straight to slightly curved, tuberculate spiny-spindles (Fig. 2.129). The short, wary rodlets are a relatively consistent length, from 0.08–0.13 mm long while the small clubs are from 0.09–0.19 mm long. Occasionally there are large spindles that can reach 0.65 mm long but most of the spiny-spindles are approximately 0.14–0.5 mm long. Small crosses with moderate tubercles occasionally occur as do small flanged spindles.

The surface of the colony has very similar sclerites to that in the calyces (Fig. 2.130). The short, warty rodlets (0.07–0.16 mm long) are again common as are clubs and straight spiny-spindles. Most of the spiny-spindles grade from 0.16–0.35 mm long, but much larger sclerites, up to 0.7 mm long, were found. Very occasionally tuberculate crosses and flanged spindles also occur.

The medulla has narrow, slightly curved or straight, sparsely tuberculate spiny-spindles (Fig. 2.131). Many are brown in colour when viewed under transmitted light and fragile so tended to be broken during the sampling procedure. The brown sclerites were significantly more common in the centre of the medulla while the narrow clear spindles were more likely to be from the outer part of the medulla. The clear spindles were usually from 0.09–0.5 mm long while the brown sclerites from the centre of the medulla were very often broken, despite multiple sampling attempts so lengths of 0.12–0.62 mm remain a probable underestimate. Fusion, branching and forking of sclerites were observed but these were not common.

Sclerites were all transparent under transmitted light except for some medulla sclerites which were light brown.

Variation:

Most of the paratypes are generally consistent in colony form and sclerite shape. One of the notable exceptions in colony form and appearance is ZMUC-ANT-000468 which is a large, branching colony, with many anastomoses, and the vertical branches merge and separate multiple times making it a much more complex colony than the holotype (Fig. 2.132A). Additionally, most of the polyps are preserved exsert rather than retracted as in the holotype (Fig. 2.132B). The extended polyps have an exposed neck region allowing the sclerite arrangement to be more easily assessed compared to the holotype (Fig. 2.132C). A longitudinal cross-section of a polyp bunch showed the terminal polyp body cavities not extending very far into the medulla, no obvious large canals and a firmly attached cortex with only small boundary canals (Fig. 2.132D). The sclerites of this paratype are similar to those of the holotype but are larger and slightly more warty, particularly in the cortex where the sclerites include large, warty spiny-spindles.

Similarly, ZMUB 60246 is a very large, robust colony consisting of many pieces, with common anastomoses and most polyps exsert (Fig. 2.133A). A small proportion of the large colony is peachy pink in colour while most of the colony is cream (Fig. 2.133B). Sclerites are similar to the holotype with the exception of rare branched and warty spiny-spindles in the points which are wartier than the holotype. Most of the polyps are exsert in the specimen ZMUB 3897 which again means the colony looks quite different to the holotype but the usual colony form of multiple, vertical, occasionally anastomosing branches emanating from an encrusting membrane is still evident (Fig. 2.133C). There are some sclerites from the points, calyx and surface which are simple spindles with thorns rather than tubercules as in the holotype. Fragments of both *L. anitorkilda* n. gen., n. sp. and *A. grandiflora* colonies were found in ZMUB 17759, with both colonies looking very similar (Fig. 2.133D). ZMUB 548 is very similar to the holotype (Fig. 2.133E) but other colonies have much more substantial anastomoses and membranous growths making the colonies complex (Fig. 2.133F, G).

As mentioned above, in the holotype and in most of the paratypes the surface of the colony between and on the calyces is a smooth mat of sclerites with most sclerites too small to be reliably discerned under a dissecting microscope. However, in the specimen ZMUB 12120 some calyces have obvious, long, longitudinally aligned spindles in an outer layer while the short, warty rodlets are common in an inner layer (Fig. 2.134A, B). This arrangement does not appear to be consistent, with some calyces having only a few long spindles obvious while others have only patches with long spindles as the dominant sclerite. As the polyp neck region invariably has a jumble of smaller spiny-spindles and rods, those polyps with long spindles as the dominant sclerite in the calyx have a clear distinction between the calyx and polyp neck. Areas of the cortex between the calyces have patches of long spindles which again are not consistent. An unregistered ZMUB specimen has a similarly patchy distribution of long spindles although it appears to have the spindles in an inner layer of the calyx with the shorter sclerites forming an outer layer.

Specimens recently collected from Trondheimsfjord, Norway, very close to the collection site of the holotype, were photographed soon after collection (Fig. 2.135A, B). For these samples, live colour varies from creamy pink to apricot, similar to those from the Gulf of Mexico. One of these samples was preserved with many polyps having the tentacles expanded (Fig. 2.135C, D). An additional in situ colony from Trondheimsfjord appears likely to be an example of this species but was not available for examination, so this must remain unconfirmed (Fig. 2.136).

A small piece of a colony collected from the east coast of Brazil is also included as a paratype (NHMUK 1917.6.7.1). The sclerites are consistent with those from the holotype and it provides more evidence that the species is widespread.

In situ photographs of the specimen TMAG K4272 from the Gulf of Mexico show an extensive colony which hanging down from an artificial structure with its many branches emanating from a membranous base (Fig. 2.137A, B) and polyps are crowded with large tentacles obvious on exsert polyps (Fig. 2.137C). Colonies are cream to beige in situ but are closer to apricot in bright surface light soon after collection (Fig. 2.137D, E) but are bleached to almost white in ethanol (Fig. 2.137F). Sclerites are similar to those of the holotype in most areas (Figs. 2.138; 2.139), although the spindles from the calyx are slightly shorter than those from the holotype (0.2–0.36 mm long in TMAG K4272 *cf*. 0.14–0.5 mm for the holotype) and sclerites from the cortex are generally stouter and have more broad tubercles than the holotype (Fig. 2.139B). Considering the geographic distance separating the Gulf of Mexico samples and Norwegian samples and that there are genetic character differences between these geographic groups (see section 2.3.3), the Gulf of Mexico specimens may represent a separate species within this genus. However, without more significant morphological differences and a stronger understanding of what is sufficient genetic variation within this group they remain within this species but are not included as paratypes.

Distribution:

Northern Atlantic—relatively common along the coast of Norway; Iceland; east coast of Brazil; Gulf of Mexico

Depth:

50–550 metres.

Remarks:

For over 150 years this species has been repeatedly mistaken for specimens of *Anthothela grandiflora.* This is understandable as the two species are sympatric, similar in colour, similar in colony form and the many of the sclerites in both species are tuberculate spiny-spindles. The initial mistake, made possibly by Sars not long after he described *A. grandiflora,* seems to have been compounded by Broch, (1912b) in his influential re-description of *A. grandiflora* where he figured what appear to be the small, warty rodlets from the calyx and cortex common in *L. anitorkilda* n.

gen., n. sp. Although stating that he viewed many specimens from a number of museums, including the holotype of *A. grandiflora*, he was not specific on exactly which specimen or specimens he figured. In his discussion he mentioned short, thick cylinders, only 0.1–0.2 mm long, as abundant in the calyces and in the colony surface (Broch 1912b). The holotype of *A. grandiflora* does not have sclerites like that but as they were figured in Broch's re-description the misconception that it does has continued for many years. Additionally, Broch mentioned that there are no sclerites in the pinnules of *A. grandiflora;* this is clearly incorrect as, in the holotype of *A. grandiflora* the pinnules are packed with long spatulate clubs; however the sclerites in the pinnules of *L. anitorkilda* n. gen., n. sp. tend to be masked by the fleshiness of the pinnules and do not always reach the tip of the pinnule so it is feasible that Broch failed to notice them. There were samples investigated for this project where the two species were still in the same jar (NTNU-VM 40341, ZMUB 17759, ZMB 5527 (determined by Broch)) and all were labelled *A. grandiflora.* These points support the hypothesis that Broch used more than one specimen in his description and at least one of these specimens was *L. anitorkilda* n. gen., n. sp. Subsequent researchers often used Broch's 1912 re-description, sometimes finding the short, warty rodlets (so possibly actually investigating a specimen of *L. anitorkilda* n. gen., n. sp.) and sometimes failing to find them (so possibly with a true *A. grandiflora* specimen). For example, Verrill (1922) in his description of *A. grandiflora* stated the figures are "from the type described in 1869", however Plate VI Fig. 1 appears to depict *L. anitorkilda* n. gen., n. sp. with the small, warty rodlets in the calyx and cortex. His description—"the cortex of the calicles and coenenchyme is finely granulous under a lens; when dried, and the surface is filled with an abundance of very irregular and pop-corn shaped spicules, with roughly warted and mostly spindle-shaped spicules beneath, mixed with some irregular clubs, rods, and many small irregular forms of various shapes" (Verrill 1922) is a good description of the sclerites found in the calices and cortex of *L. anitorkilda* n. gen., n. sp. instead of the holotype of *A. grandiflora* which has calyx and cortex sclerites which are chiefly long, narrow spindles. However, the colony depicted in Verrill's Text Fig. 2 is much like the holotype of *A. grandiflora* and not of *L. anitorkilda* n. gen., n. sp. Stiasny (1937) mentioned two colony forms in the specimens of *Anthothela grandiflora* he investigated. The first form had a flat membranous plate from which robust, upright branches with little or no anastomoses arise, much like that described here for *L. anitorkilda* n. gen., n. sp. The description of the colony form of the second specimen more closely matches that of *A. grandiflora*. The text figure of the sclerites may easily be depicting the warty rodlets from the calyces and cortex of *L. anitorkilda* n. gen., n. sp. (Text Fig. 1g–i). It is possible that the two colony forms mentioned by Stiasny actually represented the two confused species.

Considering that in every one of the six European museums visited for this study, and in collections obtained from NMNH and NHMUK, multiple, large specimens of this species were found, with most labelled as *A. grandiflora,* it seems highly likely there are more examples of this species still incorrectly identified as *A. grandiflora* in many other museums. Given that large colonies have been found in the Gulf of Mexico and noted off the coast east coast of the USA (Scott France, pers. comm.) combined with the many examples examined from Norway and the slender evidence of a presence off the east coast of Brazil it would seem to have a widespread distribution in the Atlantic Ocean.

Etymology:

The name is a derivation in honour of **Ani**ta Kaltenborn and Dr **Torkild** Bakken from NTNU-VM, Trondheim, Norway who provided samples, enthusiasm and encouragement, and were the first to suspect an overlooked species. Noun in apposition.

2.3.3 Genetic relationships among morphospecies of *Anthothela*, *Victorgorgia* and *Lateothela* n. gen.

2.3.3.1 Sequencing success and alignment

From the 90 specimens used in the morphological study, a total of 30 sequences were obtained for the mtMutS region and 26 for the igr1-COI region (Table 2.4). Despite multiple attempts and the use of internal primers, some specimens could not be successfully amplified and/or good quality sequences could not be obtained despite the fact that they were from relatively recent collections.

For mtMutS, sequences varied from 458 to 965 nucleotides long (Table 2.4), the length variation mostly due to the poor quality of DNA. Of those 30 sequences, 7 were shorter than 500 base pairs long with only mtMutSA or mtMutSB successfully sequenced with the internal primers. The longest sequences included the ND4 region upstream of mtMutS (obtained when using the ND42475F primer) but analyses were conducted on trimmed sequences without the ND4 region. After restricting the taxa to only those included in the detailed morphological systematics assessment and including externally obtained sequences of examined specimens, 31 sequences remained. Alignment (excluding the outgroup sequences) was unambiguous with no insertions or deletions. Once the sequences were aligned, the total length for the sequences in the analyses was 976 base pairs, with most sequences missing some portions of the full length. All sequences were then trimmed to a total length of 772 nucleotides. Within the final alignment of 31 sequences, 100 positions were variable with 74 parsimony informative sites (Table 2.5).

For igr1–COI, sequences varied from 532 to 1023 nucleotides long (Table 2.4). Again, there were 3 specimens where only igr1–COIA or igr1–COIB was able to be sequenced with the internal primers.

After restricting the taxa to only those included in the detailed morphological systematics assessment and including externally obtained sequences of examined specimens, 28 sequences remained. There were no insertions or deletions with alignment unambiguous (excluding outgroup sequences). All sequences were trimmed to a total length of 930 nucleotides. Within the final alignment, 51 positions were variable with 40 of those parsimony informative (Table 2.5).

Table 2.4. Taxa for which sequences of mtMutS and igr1–COI were obtained, the number of specimens where amplification was attempted and the number of sequences obtained with the range of sequence lengths.

Taxa	Attempted	mtMutS		igr1–COI	
		Sequenced	Length (bp)	Sequenced	Length (bp)
Anthothela grandiflora	7	5	458–808	5	837–1023
Anthothela vickersi	10	8	482–822	6	537–970
Anthothela aldersladei	3	1	476	1	540
Victorgorgia eminens	7	5	782–965	4	532–1019
Victorgorgia nyahae	2	2	837–922	2	961–977
Lateothela anitorkilda	4	4	768–821	4	916–947
Anthelia fallax	1	1	787	1	886
Clavularia borealis	2	2	792–813	2	962–968
Trachythela rudis	3	2	518–763	1	910
Total	**39**	**30**		**26**	

2.3.3.2 Genetic distances as support for morphological decisions

Nucleotide variation and mean genetic distance indicated that the gene region mtMutS was more variable than igr1–COI for most groups and in most comparisons (intraspecific, intrageneric and intergeneric variation) (Table 2.5). The two gene regions concatenated had more parsimony informative sites than the individual gene regions but were found to have similar or slightly lower genetic distances to that obtained using mtMutS only. Initial analysis indicated that there were large genetic distances between the specimens which were all supposedly *Anthothela,* so the analysis was repeated with the specimens grouped such that within-group mean p-distances were no greater than 1.1% (mtMutS only) forming hypothetical genera. The hypothetical genera matched precisely with the three easily discernible groups or genera found using morphological assessment; that is *Anthothela, Victorgorgia* and *Lateothela* n. gen.

Pairwise mean p-distances between the hypothetical genera (intergeneric distances) were between 0.020 (2%) and 0.077 (7.7%) (Table 2.5) which are comparable or higher than intrafamilial intergeneric ranges found previously using the same gene regions (Baco & Cairns 2012; McFadden, Alderslade, et al. 2006; McFadden & van Ofwegen 2012a).

In general, intrageneric genetic differences were very small and there was usually no discernible threshold indicative of interspecific versus intraspecific genetic distances, making species delineations based on genetic distances only, inconclusive. Within-group mean p-distances (interspecific distances) were very low within *Anthothela* (0.000–0.007, 0–0.7%) while *Lateothela* n. gen*.* has only a single morphospecies so could not be accessed for interspecific variation (however see below for an assessment of genetic variation corresponding to geographic separation within this genus). For *Victorgorgia* the interspecific mean p-distance was 0.018 (1.8%), (Table 2.5) reflecting some unexpected sequence divergence in *V. nyahae* n. sp., specifically within the mtMutS gene region.

V. nyahae n. sp. is represented by two specimens that are morphologically very similar but which have 24 nucleotide differences and a pairwise mean p-distance of 0.029 (2.9%) in the mtMutS region alone, a p-distance significantly higher than any conspecific genetic distance found by McFadden et. al (2011) or Baco & Cairns (2012) and also significantly higher than any intraspecific variation found within. Both specimens were extracted on two different occasions and each gene region was amplified and sequenced three times but the relatively large differences between the two specimens in the mtMutS gene region were maintained. Nevertheless, they have been kept as one species here given that they are consistently positioned together in a single well-supported clade (see below), given that the igr1–COI region from the same species does not contain comparable differences and given their very similar morphology and location, being from the same seamount (see *V. nyahae* n. sp. description). One specimen was collected with numerous fragments of another unrelated octocoral and there may be some remnant contamination present; however it seems unlikely that this would be the DNA amplified from both extractions. The reason(s) for these anomalous genetic sequences remains obscure and would ideally require examination of further samples of this species for final verification. When the most distant of the *V. nyahae* n. sp. specimens is excluded, the interspecifc mean p-distance for *Victorgorgia* (i.e. between *V. eminens* n. sp. and the remaining *V. nyahae* n. sp. specimen) is 0.008, less than the suggested genetic distance threshold indicative of congenerics.

Genetic distances among morphospecies (intraspecific distances) were otherwise very low, especially within *Anthothela* and *Lateothela* n. gen. where sequences were identical or differed by only a few base pairs (Table 2.5).

Table 2.5. Summary statistics for sequences included in first phylogenetic analysis (restricted to specimens included in the detailed morphological assessment but includes sequences generated in this project plus other studies). Resolution of morphospecies is based on strong phylogenetic support for monophyly. [specimens which lacked full length sequences were excluded from # bp differences]

		mtMutS	**igr1–COI**	**mtMutS–igr1–COI concatenated**
No. of sequences in analysis		31	28	27
Analysed sequence length		772	930	1680
No. of variable sites		100	51	153
No.of parsimony informative sites		74	40	112
No. of morphospecies resolved		5 of 7	5 of 7	6 of 7
Morphospecies not resolved		*A. vickersi/A. grandiflora/A. aldersladei*	*A. vickersi/A. grandiflora* *V. nyahae/V. eminens*	*A. vickersi/A. grandiflora*
% resolved		71%	71%	86%
Intergeneric mean p-distances	*Anthothela–Lateothela*	0.049	0.020	0.035
(# bp differences)		(40–44)	(18–24)	(56–74)
	Anthothela–Victorgorgia	0.066	0.031	0.055
		(55–83)	(29–38)	(76–121)
	Lateothela–Victorgorgia	0.077	0.023	0.060
		(58–83)	(29–41)	(86–126)
Intrageneric mean p-distances	*Anthothela*	0.000–0.007	0.000–0.007	0.000–0.007
(# bp differences)		(0–10)	(0–6)	(0–13)
	Victorgorgia	0.017	0.003	0.018
		(18–38)	(4–6)	(22–44)
	Lateothela	NA	NA	NA
Intraspecific mean p-distances	*A. grandiflora*	0.000	0.000	0.000
(# bp differences)		(0–1)	(0)	(0–1)
	A. vickersi	0.001	0.000	0.000
		(0–1)	(0)	(0–1)
	A. aldersladei	NA	NA	NA
	A. quattriniae	NA	NA	NA
	L. anitorkilda	0.000	0.003	0.001
		(0–1)	(0-7)	(0–8)
	V. eminens	0.002	0.000	0.002
		(0–2)	(0–1)	(0–3)
	V. nyahae	0.029	0.005	0.015
		(24)	(7)	(31)

2.3.3.3 Phylogenetic analyses as support for morphological decisions

The concatenated gene regions generated a phylogenetic consensus tree which indicated monophyly for 6 of the 7 morphospecies for which both gene regions were available, while use of the gene regions individually resolved 5 of the 7 morphospecies for which those sequences were available (Table 2.5). For the concatenated dataset of mtMutS and igr1–COI, Bayesian and maximum-likelihood (ML) analyses returned very similar topologies and were combined into a single tree (Fig. 2.140), although the Bayesian analysis provides greater resolution in places. Most of the nodes which were well supported in the Bayesian analysis were present in the ML analysis but with slightly lower support.

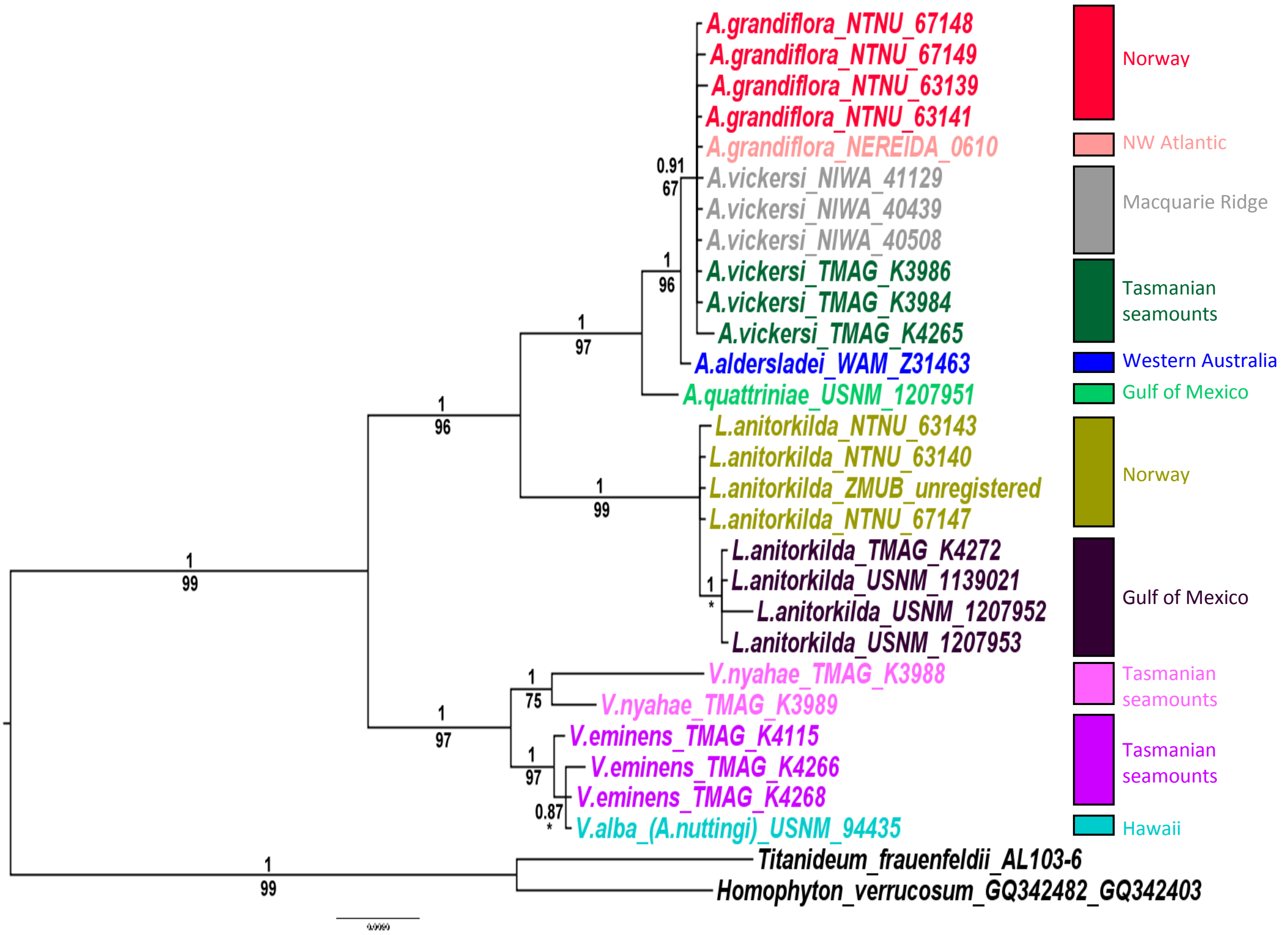


Figure 2.140. Tree generated from the concatenation of nucleotide sequence for the mitochondrial gene regions mtMutS and igr1–COI of *Anthothela*-like specimens. Bayesian posterior probabilities shown above branch, ML bootstrap values below branch; HKY+G (Bayesian results split freq = 0.0014, 6000000 gen, burnin=15000). (* indicates nodes present only in Bayesian analysis)

Three distinct, well-supported groups were consistently recognised using both approaches and were in direct concordance with the generic groupings found using morphological methods and genetic distances. One group has specimens determined morphologically as *Anthothela grandiflora,* and, as this is the type species for the genus, makes this group 'true' *Anthothela.* It is well-supported in both phylogenetic analyses. A second group, comprised of specimens morphologically determined as *Victorgorgia,* is well-supported and quite genetically distant from the *Anthothela* group. The third group contains specimens morphologically determined as *Lateothela* n. gen. and forms a well-supported clade in both analyses (Fig. 2.140). Phylogenetic analyses of the gene regions separately allowed the inclusion of additional taxa which were excluded from the concatenated analyses if one of the two gene regions were not sequenced successfully for a specimen or if both gene regions were not available in GenBank. Analyses of the two gene regions separately presented similar clades to the concatenated trees but with less resolution or lower support (Fig. 2.141, Appendix 1). Analysis of the mtMutS gene region alone did not resolve *A. aldersladei* n. sp. from the *A. grandiflora/A. vickersi* clade, while two geographic groups detected within *L. anitorkilda* n. gen., n. sp. in the Bayesian concatenated analysis (also evident in the tree generated using igr1–COI region alone (Appendix 1)) were not detected with the mtMutS region alone (Fig. 2.141). Notable specimens included in the mtMutS analysis only were an additional specimen from the north west Atlantic, determined as *A. grandiflora,* which grouped with the *A. grandiflora/A. vickersi* clade; an undetermined specimen also from the north west Atlantic, originally thought to be an *Anthothela* specimen (S. France pers. comm.) which grouped with the *L. anitorkilda* n. gen., n. sp. clade; and an additional specimen from Hawaii, determined as *A. nuttingi* (*V. alba*), which also grouped as expected with the *Victorgorgia* clade (Fig. 2.141).

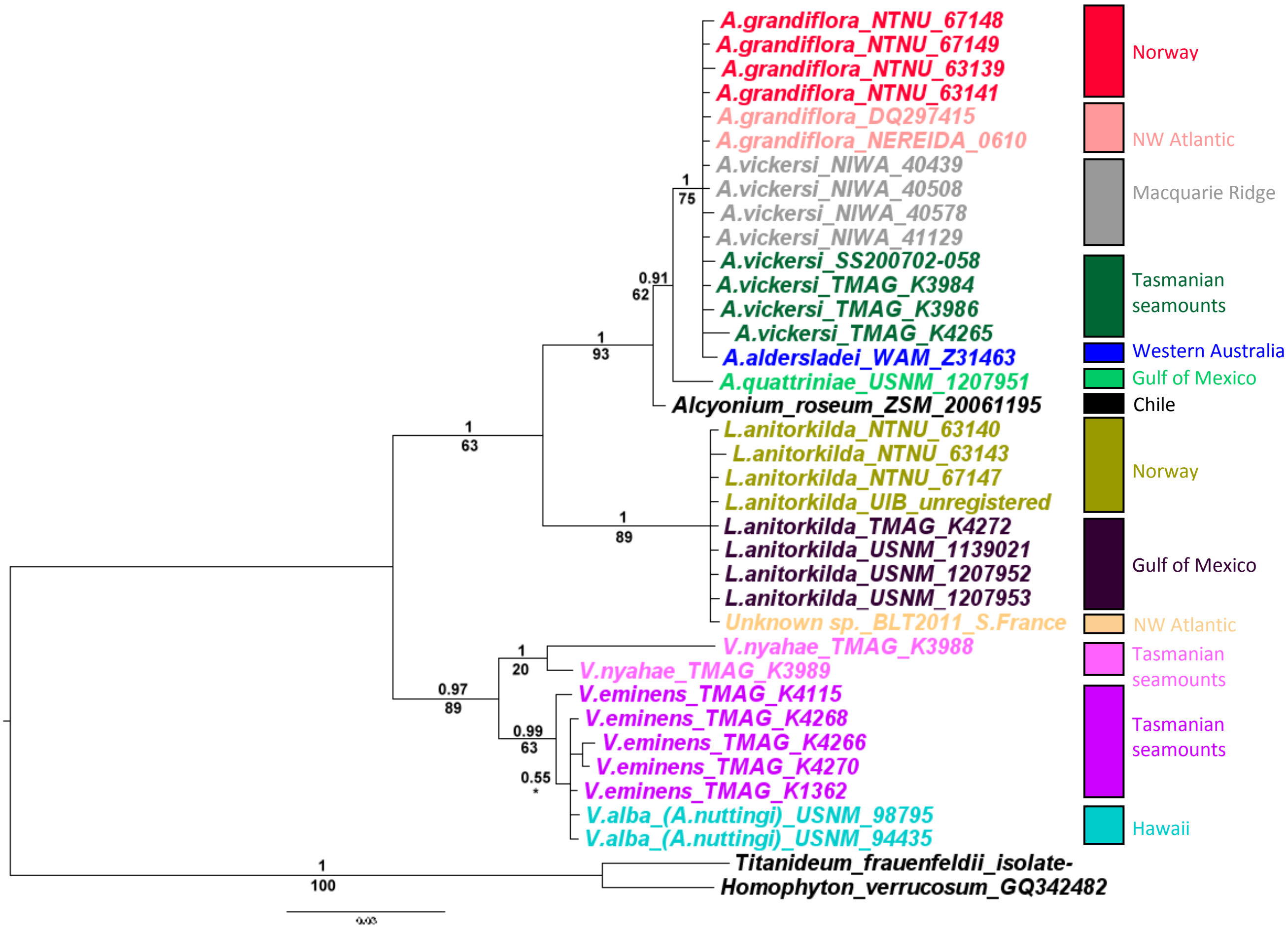


Figure 2.141. Tree generated from the nucleotide sequence for the mitochondrial gene region, mtMutS of *Anthothela*-like specimens. Bayesian posterior probabilities shown above branch, ML bootstrap values below branch; HKY+G (Bayesian results split freq = 0.002, 3000000 gen, burnin=7500). (* indicates nodes present only in Bayesian analysis)

2.3.3.4 Character-based analysis, cladistic evidence and morphology combined for species delineation

Robust taxonomic decisions require multiple, preferably independent lines of support and evidence. Increasingly, character-based analysis of sequences has been used as an additional tool in species discovery or delineation particularly in circumstances with low levels of divergence and cryptic species (Baco & Cairns 2012; McFadden et al. 2011; Rach, DeSalle, Sarkar, Schierwater, & Hadrys 2008). Unfortunately, such analysis within this study is hampered by low numbers of specimens and incomplete sequences. Nevertheless, within all genera examined, some investigation of single nucleotide polymorphisms was informative especially in relation to nodes apparent in the phylogenetic reconstructions and morphological distinctions.

Anthothela clade

Three haplotypes were detected from the 13 available concatenated sequences within the *Anthothela* clade (Table 2.6). The two morphospecies *A. grandiflora* and *A. vickersi* shared a single haplotype (H1), despite being from disparate parts of the world (Norway, eastern Canada and southern Australia) and having clearly discernible morphological differences (see section 2.3.2). They remain indistinguishable using these two mitochondrial gene regions, having identical sequences and being consistently grouped as an undifferentiated clade in both phylogenetic analyses (Figs. 2.140; 2.141). They have been retained as separate species based on morphological and geographical differences but await further research on alternate gene regions for clarification of these taxonomic units. The remaining two haplotypes within the *Anthothela* clade were unique, found from single specimens only (*A. aldersladei* n. sp. (H2) and *A. quattriniae* n. sp. (H3)). *A. quattriniae* n. sp. differed in 13 nucleotide positions from the H1 haplotype and in 12 nucleotide positions from H2, is consistently well-supported on a separate node from the other *Anthothela* species (Fig. 2.140) and has significant morphological differences. *A. aldersladei* n. sp. differed from the H1 haplotype by only a single nucleotide (in that nucleotide position matching the *A. quattriniae* n. sp. haplotype (Table 2.6, position 891)). However, only short sequences using the internal primers were successfully sequenced for this specimen of *A. aldersladei* n. sp. (mtMutSB and igr1–COIA) so further nucleotide differences are possible but could not be determined here. Morphological and geographical differences based on three *A. aldersladei* n. sp. specimens clearly separate *A. aldersladei* n. sp. from other *Anthothela* specimens and despite only a single nucleotide difference it is consistently positioned on a well-supported separate node in the concatenated and single gene region igr1–COI Bayesian phylogenetic analyses (Fig. 2.140 & Appendix 1). However, the node was not present in the phylogenetic reconstructions using the single gene region mtMutS (Fig. 2.141). Full sequences of the gene regions and additional specimens would provide a more robust assessment of the morphological decision.

Table 2.6. Single nucleotide differences between haplotypes within the *Anthothela* clade.

			mtMutS						igr1–COI						
Morphospecies	**Haplotypes**	**n**	**164**	**199**	**220**	**517**	**558**	**559**	**700**	**891**	**1095**	**1298**	**1446**	**1545**	**1730**
A. grandiflora	H1	5	C	C	C	A	C	A	C	A	A	G	G	G	G
A. vickersi	H1	6	C	C	C	A	C	A	C	A	A	G	G	G	G
A. aldersladei	H2	1	?	?	?	A	C	A	C	G	A	G	?	?	?
A. quattriniae	H3	1	T	T	T	C	T	G	T	G	C	A	A	A	A

Lateothela n. gen. clade

This clade is made up of eight specimens morphologically and genetically distinct from *Anthothela* and *Victorgorgia* (section 2.3.2 and Figs. 2.140; 2.141). Of the eight specimens, four were collected from the Norwegian coastline and four from the Gulf of Mexico—two widely separated geographic regions. Four haplotypes were detected, two from Norway and two from the Gulf of Mexico (Table 2.7), however two of those haplotypes were dominant (H2 & H3), each occurring in three specimens and each representing the geographic regions. The three parsimonious informative sites between these two haplotypes were all found in the igr1–COI marker (all the eight specimens were identical at the mtMutS marker except for a single nucleotide in one specimen (H1)). Bayesian analysis of the concatenated gene regions grouped the Gulf of Mexico samples in a separate clade from the Norwegian specimens while the ML analysis showed no distinction between the geographically separated specimens (Fig. 2.140). The two geographic groups, with a between-group mean genetic distance of 0.002 (0.2%), three nucleotide differences and no significant or consistent morphological differences (section 2.3.2), are retained here as "genetically [and geographically] distinct populations" of the same species (McFadden & van Ofwegen 2012b). The fourth unique haplotype was from a specimen from the Gulf of Mexico that varied from all the other specimens in four additional sites but remains grouped with the other specimens in both the Bayesian and ML analysis as these sites do not appear to be phylogenetically significant.

Table 2.7. Single nucleotide differences between haplotypes within the *Lateothela* n. gen. clade.

			mtMutS	igr1–CO1						
Morphospecies	**Haplotypes**	**n**	**655**	**774**	**1285**	**1421**	**1431**	**1462**	**1569**	**1723**
L. anitorkilda (Norway)	H1	1	T	C	G	T	C	G	T	T
L. anitorkilda (Norway)	H2	3	C	C	G	T	C	G	T	T
L. anitorkilda (Gulf of Mexico)	H3	3	C	T	G	C	A	G	T	T
L. anitorkilda (Gulf of Mexico)	H4	1	C	T	A	C	A	A	A	C

Victorgorgia group

For *Victorgorgia* the mtMutS region was found to be considerably more variable than igr1–COI but this is confounded by relatively massive differences between the two specimens of *V. nyahae* n. sp.

(Table 2.8). Analysis of the mtMutS sequence alone allowed the inclusion of specimens for which only mtMutS sequences were available, including a second specimen from Hawaii. Using the mtMutS gene region four haplotypes were detected within the *Victorgorgia* group. One haplotype (H1) was shared between specimens of *V. eminens* n. sp. from southern Australia and two specimens from Hawaii determined as *A. nuttingi* (=*Clematissa alba*=*V. alba*). The morphology of one of these Hawaiian specimens does not correspond to that of the type specimen of *V. alba* but it is similar to *V. eminens* n. sp. (see section 2.3.2). These geographically distant specimens form a single well-supported clade in all the phylogenetic reconstructions (Figs. 2.140; 2.141 and Appendix 1) (differences in sequence length are reflected in branch lengths). There are no consistent genetic or morphological differences between examined specimens from Tasmania and Hawaii, however morphological examination was possible on only a small fragment of a colony from Hawaii so future assessment of whole colonies may illuminate morphological differences which coincide with geographical placement. Two specimens of *V. eminens* n. sp. from southern Australia displayed a different haplotype (H2), differing from H1 by only a single nucleotide in the mtMutS marker (Table 2.8, position 557). No morphological or geographical differences were observed between these samples and other *V. eminens* n. sp. samples and this SNP is assumed to be intraspecific variation.

Table 2.8. Single nucleotide differences between haplotypes within the *Victorgorgia* clade.

			mtMutS																		
Morphospecies		**n**	**15**	**28**	**42**	**48**	**76**	**123**	**138**	**142**	**159**	**166**	**169**	**204**	**223**	**271**	**302**	**322**	**327**	**339**	**356**
V. alba (Hawaii)	H1	2	T	A	G	T	C	T	A	T	A	G	T	T	G	T	A	C	G	A	A
V. eminens (S.Aust)	H1	3	T	A	G	T	C	T	A	T	A	G	T	T	G	T	A	C	G	A	A
V. eminens (S.Aust)	H2	2	T	A	G	T	C	T	A	T	A	G	T	T	G	T	A	C	G	A	A
V. nyahae K3989	H3	1	C	A	A	T	C	T	A	T	A	A	T	A	T	T	A	T	A	A	A
V. nyahae K3988	H4	1	T	G	A	C	T	C	G	C	G	A	C	A	T	A	G	T	G	G	G

			mtMutS continued																	
Morphospecies		**n**	**379**	**388**	**414**	**557**	**575**	**597**	**617**	**648**	**654**	**659**	**666**	**668**	**673**	**679**	**687**	**762**	**766**	
V. alba (Hawaii)	H1	2	C	A	A	G	G	A	C	T	C	T	T	T	A	G	A	A	A	C
V. eminens (S.Aust)	H1	3	C	A	A	G	G	A	C	T	C	T	T	T	A	G	A	A	A	C
V. eminens (S.Aust)	H2	2	C	A	A	A	G	A	C	T	C	T	T	T	A	G	A	A	A	C
V. nyahae K3989	H3	1	T	G	A	A	G	G	T	T	T	T	T	C	A	A	A	A	G	C
V. nyahae K3988	H4	1	T	G	G	A	T	G	T	C	T	C	A	T	T	A	T	C	G	T

			igr1–COI						
Morphospecies		**n**	**1079**	**1490**	**1493**	**1521**	**1547**	**1580**	**1595**
V. alba (Hawaii)	H1	2	T	T	C	A	A	A	T
V. eminens (S.Aust)	H1	3	T	T	C	A	A	A	T
V. nyahae K3989	H2	1	T	T	C	C	G	G	T
V. nyahae K3988	H3	1	A	C	T	A	A	A	G

The two *V. nyahae* n. sp. samples, as mentioned above, have 24 variable nucleotide positions between them in the mtMutS gene regions alone (and 7 differences in the igr1–COI gene region) (Table 2.8) forming the remaining two haplotypes detected in *Victorgorgia* (H3 & H4). Despite this they are grouped in a single clade, as a sister group to *V. eminens* n. sp. in the concatenated phylogenetic reconstructions (Fig. 2.140). Given that no significant morphological differences were observed and given that they were collected from the same seamount, this large sequence divergence between these two specimens is unexpected and requires further investigation.

2.3.3.5 The polyphyletic nature of Anthothelidae, phylogenetic relationships with other genera, and the position of species previously confused with Anthothela

Additional sequences were included in a second analysis to elucidate relationships between the studied genera and other Octocorallia genera. In general this phylogenetic tree is disorganized and poorly resolved (more sequences representing each genus would probably allow a clearer tree), however the distinct clades of the genera within this study remained well supported (Fig. 2.142). All sequences available from the species currently included in the family Anthothelidae were included and highlighted according to the subfamilial groups. The family Anthothelidae is shown to be highly polyphyletic, including specimens from both sides of the deep node of the tree, although two of the subfamilies may be monophyletic. The genera *Titanideum*, *Homophyton* and *Diodogorgia*, all from the subfamily Spongiodermatinae, appear to form a monophyletic clade associated with the smaller Calcaxonia–Pennatulacea (plus *Anthomastus* and Parasphaerascleridae) clade described in McFadden et al. (2006). The genera *Iciligorgia* and *Solenocaulon*, from the subfamily Semperininae also form a single clade. However, the third subfamily Anthothelinae is shown to be highly polyphyletic including *Erythropodium caribaeorum* situated with the Calcaxonia–Pennatulacea clade, and three other available genera of the subfamily found in three different distant clades within the Holaxonia–Alcyoniina clade (McFadden et al. 2006) (Fig. 2.142). The new genus *Lateothela* was found to be more closely related to the genus *Alcyonium* from the family Alcyoniidae than to any of the genera from Anthothelinae. It remains unplaced to subfamily.

The genera *Anthothela* and *Lateothela* n. gen. were found to be very closely related to some nominal *Alcyonium* specimens (Fig. 2.142). One of the sequences is from *Alcyonium varum* McFadden & Ofwegen, 2013 (was *Alcyonium roseum* van Ofwegen, Häussermann & Försterra, 2007)) which is genetically and morphologically very similar to *Anthothela* specimens. It differs from *Anthothela* species by mean p-distances of 0.003–0.007 (0.3–0.7%) (6 parsimony informative sites between *Alyconium varum* and all other *Anthothela* species with the concatenated gene regions), which is only slightly more than the threshold value of 0.3% genetic distance for species discrimination among *Alcyonium* species (McFadden, Brown, et al. 2014) but much lower than the genetic distance which could be expected of a species currently in a different family (and sub-ordinal group) to *Anthothela.* Morphologically, sclerites from *Alcyonium varum* are very similar to those of other *Anthothela* species but colony forms are different (*Alcyonium varum* is membranous only with small clumps of polyps while *Anthothela* species usually have branches and form complex upright colonies with a scleraxonian axis). Another *Alcyonium* species, *Alcyonium haddoni* Wright & Studer, 1889, a southern hemisphere species used as an outgroup in McFadden et al. (2011), was found to be more closely related to *Alcyonium varum* and the *Anthothela* specimens than the other *Alcyonium* species included. The colonies and sclerites of *Alcyonium haddoni* as described in van Ofwegen, Häussermann & Försterra (2007) appear to differ from those of *Anthothela* but a detailed comparison of this and closely related *Alcyonium* species (such as *Alcyonium patagonicum* (May, 1899)*, Alcyonium jorgei* van Ofwegen, Häussermann & Försterra, 2007, *Alcyonium yepayek* van Ofwegen, Häussermann & Försterra, 2007 and *Alcyonium glaciophilum* van Ofwegen, Häussermann & Försterra, 2007 which all form a clade with *A. haddoni* (McFadden pers. comm.)), may prove informative.

Lateothela anitorkilda n. gen., n. sp. was found to be most closely related to nominal *Alcyonium* species, particularly *Alcyonium grandiflorum* Tixier-Durivault and d'Hondt, 1974 which grouped within the *Lateothela* clade (although only the mtMutS sequence was available). McFadden et al. (2011; 2001) found (mainly northern hemisphere) specimens, which have been determined as *Alcyonium,* form a number of distinct clades so two representatives from some of these clades were included here to elucidate the relationship with *Lateothela* n. gen. specimens. *Alcyonium digitatum* and *Alcyonium* sp. A (and *Gersemia*) are separate to all the other *Alcyonium* specimens as well as to the *Anthothela* and *Lateothela* n. gen. clades (Fig. 2.142). *Lateothela* n. gen. forms a well-supported clade which is a sister group to the *Alcyonium* clade consisting of *Alcyonium glomeratum/ Alcyonium acaule*/ *Alcyonium palmatum* and *Alcyonium rubrum* and these two clades share a node with another *Alcyonium* clade consisting of *Alcyonium bocagei*/ *Alcyonium spM2*/ *Alcyonium coralloides*. The single specimen of *Alcyonium variabile* is basal to that node. The placement of these species suggests an entwined relationship between what is understood to be *Alcyonium* species and *Lateothela* n. gen. In fact, *Lateothela* n. gen*.* is considerably closer genetically to most nominal *Alcyonium* species than to *Anthothela* despite having a colony form very similar to *Anthothela* (although the sclerites from *Lateothela* n. gen*.* are similar to those in some nominal species of *Alcyonium*). This is probably a reflection of the recognised diverse and complicated nature of the genus *Alcyonium* and may signal a need to reassess the traditional taxonomic importance given to colony form, with sclerites perhaps a better indicator of phylogenetic relatedness.

The reassignment of *Trachythela rudis* to *Clavularia* by Deichmann (1936) was not well defended and did not involve an examination of the type specimen thus the species should remain in *Trachythela.* Specimens which were identified morphologically as *Trachythela rudis* (=*Clavularia rudis*) were from southern Tasmania, Australia, the Rehoboth Seamount, NW Atlantic and the Gulf of Mexico and the morphological and molecular differences (within-group mean p-distance of 0.001) between them are slight suggesting they may represent a single well-distributed species. *T. rudis,* although only occurring as a membranous colony, is superficially morphologically similar to *Anthothela,* however both molecular and morphological evidence demonstrate it is quite distinct (Fig 2.142; Table 2.10). It is closer genetically to another encrusting species included in this analysis, *Clavularia borealis* (=*Anthelia borealis*), and to specimens from the genus *Victorgorgia.* However, there is significant uncertainty regarding the placement of *Trachythela* as it was shown to be genetically distant from other stoloniferan genera (McFadden & van Ofwegen 2012c). The relatively close genetic relationship of these two encrusting species with *Victorgorgia* is counterintuitive to the morphological differences and requires further research, although interestingly all three genera seem to be represented by specimens which are variations of purple when alive.

The two species *Clavularia borealis* (=*Anthelia borealis*) and *Anthelia fallax* Broch, 1912, have previously been confused with *Anthothela.* Although these two species are potentially from the same genus according to the literature, they are understood to be incorrectly placed and in need of revision. The genus *Anthelia* is within the family Xeniidae with well-defined characteristics very distinct from those found in *C. borealis* or *Anthelia fallax.* Sequences from specimens determined morphologically as *C. borealis* and *Anthelia fallax* after comparison with the relevant type material, have a mean pairwise p-distance of 0.033 supporting the supposition they represent different genera and both are placed distant to true Xeniidae specimens (Fig. 2.142). A small clade of the two specimens of *C. borealis* had very strong support and is significantly distant from *Anthothela* (pairwise p-distance of 0.064) which supports the morphological differences found between *C. borealis* and *Anthothela* specimens (see section 2.3.4). The single sequence from a specimen of *Anthelia fallax* tended to slightly change phylogenetic position depending on the model or analysis method employed but remains distinct from all other specimens included here and usually basal to the branch of *Victorgorgia, T. rudis* and *C. borealis* (Fig. 2.142). This specimen is also genetically distant from *Anthothela* (mean pairwise p-distance of 0.045) and morphologically different (see section 2.3.4). The correct taxonomic position for these species remains unclear.

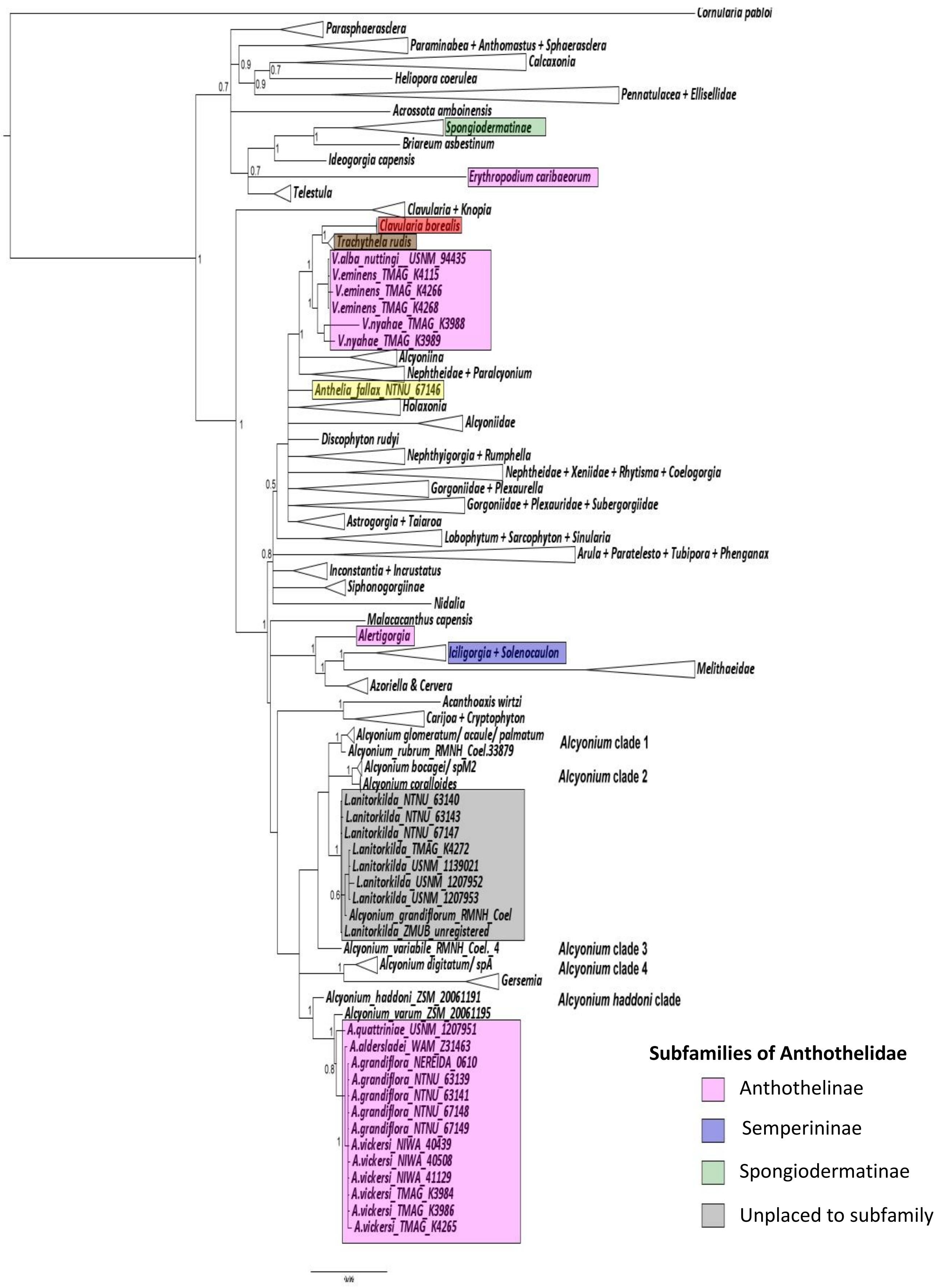


Figure 2.142. Bayesian tree generated from the concatenation of nucleotide sequence for the mitochondrial gene regions mtMutS and igr1–COI for most Octocorallia genera. Genera in the family Anthothelidae and species previously confused with *Anthothela* are highlighted in coloured boxes*.* Major *Alcyonium* clades from McFadden et al. (2011)) indicated with adjacent labels. Bayesian posterior probabilities shown; GTR+G+I model (Bayesian results split freq = 0.004, 10000000 gen, burnin=25000).

2.3.4 Remarks on the morphology of species historically confused with *Anthothela*

Species which have been suggested to be *Anthothela* in the literature, species previously mistaken for *Anthothela* and species suspected to be *Anthothela* due to a similar morphology were examined where possible as part of the review of *Anthothela*. Very few of these species were found to be *Anthothela* (Table 2.10) with the exception of *Spongioderma (?) vickersi*. *Gymnosarca bathybius* Kent, 1870 was the only species for which a type specimen could not be located so it remains as an unconfirmed synonym of *Anthothela grandiflora.* The type specimens of *Anthelia fallax, Clavularia borealis* (=*Anthelia borealis*)*, C. griegii, C. eburnea* Kükenthal, 1906*, Iciligorgia boninensis* Aurivillius, 1931*, Stereogorgia claviformis* Kükenthal, 1916, *Suberia köllikeri* Studer, 1878 (=*Semperina köllikeri*=*Iciligorgia köllikeri*), *Trachythela rudis* (=*Clavularia rudis*) and *Rhizoxenia alba* (=*Clavularia alba*) Greig, 1887 were all examined for the revised characteristics of *Anthothela.* Many of these species remain uncertainly placed and redescriptions and revisions of the genera are badly needed.

Table 2.10. Species which have been or could be mistaken for species of *Anthothela.*

Species	**Author**	**Reason for inclusion**	**Current placement By whom**	**Specimen examined**	**Differences with *Anthothela***
Gymnosarca bathybius	Kent, 1870	Has been synonymised with *A. grandiflora* by many authors	*?A. grandiflora* Kükenthal 1924	Type not located	Remains unconfirmed
Suberia köllikeri	Studer, 1878	Similar morphology	*Iciligorgia köllikeri* Grasshoff 1999	Holotype	Polyps restricted to one side of colony, low calyces, heavily warty, oval spindles in calyx and cortex
Clavularia borealis	Koren & Danielessen, 1883	Placed as a variation of *A. grandiflora* by Molander (1918)	*Anthelia borealis* Broch 1912	Holotype	Membranous, lacks spatulate clubs in tentacles, pinnules have sparse, narrow rods, purple
Rhizoxenia alba	Greig, 1887	Molander (1915) placed it "among *A. grandiflora"*	*Clavularia alba* Hickson 1894	Holotype	Only stolons remaining with small warty sclerites, according to literature transverse sclerites in tentacles
Clavularia eburnea	Kükenthal, 1906	Molander (1929) suggested it may be a "Scleraxonia (Briareidae?)"	*Clavularia eburnea*	Holotype	Lacks spatulate clubs in tentacles, has torch clubs in tentacles, points, neck and calyx, has heavily ridged calyces, medulla unconfirmed
Anthelia fallax	Broch, 1912	Variation of *A. grandiflora* by Molander (1918)	*Anthelia fallax*	Syntypes	No calyx, membranous only, bright yellow (has spatulate clubs in pinnules)
Stereogorgia claviformis	Kükenthal, 1916	Similar morphology	*Stereogorgia claviformis*	Holotype	Central axis is a hard lattice
Trachythela rudis	Verrill, 1922	Similar morphology	*Clavularia rudis* Diechmann 1936	Holotype	Lacks spatulate clubs in tentacles, pinnules have narrow, mostly smooth, sharply bent spiny-spindles, purple
Iciligorgia boninensis	Aurivillius, 1931	Not normally a deep-sea genus and similar morphology	*Iciligorgia boninensis*	Holotype	Long needles in medulla, fistulous branch tips, likely true *Iciligorgia*
Clavularia griegii	Madsen, 1944	Similar morphology	*Clavularia griegii*	Holotype	Lacks spatulate clubs in tentacles, distal tip of pinnules packed with jumbled short, flat rods

2.4 Key to the subfamily Anthothelinae

A key to the genera of the nominal subfamily *Anthothelinae* is provided but many questions remain, especially the entangled molecular relationships of *Alcyonium, Anthothela* and *Lateothela* n. gen. and the significant genetic distance between *Anthothela* and *Victorgorgia* that suggests they belong in different families. A key to species within the studied genera was deemed ineffectual given the importance of qualitative sclerite form in distinguishing species and the heavy reliance on illustrations for differentiation.

1.	A. Polyps fully retractile into slit-like apertures	*Alertigorgia* Kükenthal, 1908
	B. Prominent calyces present	2
2.	A. Colonies with large, well-defined canals in central medulla, or hollow central medulla	3
	B. Colonies with no or indistinct canals in central medulla	5
3.	A. Hollow central medulla, smooth medulla sclerites	*Tubigorgia* Pasternak, 1985
	B. Medulla with central canals but not hollow, medulla sclerites with tubercles and warts	4
4.	A. Thick cortex with inner spongy layer, indistinctly separated from the medulla, calyces very low, sclerites include tuberculate capstans	*Briareopsis* Bayer, 1993
	B. Cortex thin, clearly delineated from medulla by large boundary space, calyces obvious, tuberculate capstans absent, josephinae clubs in pinnules and tentacles	***Victorgorgia***
5.	A. Membranous only, medulla sclerites red, 6 radiates present	*Erythropodium* Kölliker, 1865
	B. Sclerites of medulla colourless, 6 radiates absent	6
6.	A. Sclerites in pinnules and tentacle rachis are short, flat rods	***Williamsius* n. gen.**
	B. Sclerites in pinnules and tentacle rachis long spatulate clubs or spiky josephinae clubs	7
7.	A. Spatulate clubs common in pinnules, sclerites of calyx and surface predominantly tuberculate spiny-spindles	***Anthothela***
	B. Spiky, josephinae clubs in pinnules and tentacle rachis, sclerites of calyx and surface include many short, thick, warty rodlets	***Lateothela* n. gen.**

2.5 Discussion

This review of the genus *Anthothela* has found that the genus, as it has traditionally been understood, is a combination of species from four genera. Morphological delineation of the four genera has been found to be unambiguous and three of those genera are completely consistent with well-supported clades found in all phylogenetic analyses.

Following revision, the genus *Anthothela* now consists of six described species—these consist of three previously described species, *A. grandiflora, A. pacifica, A. tropicalis*; one reassigned species, *A. vickersi* (was *Spongioderma* (?) *vickersi*) and two newly described species, *A. aldersladei* and *A. quattriniae*. Transferred out of *Anthothela* to *Victorgorgia* are *A. argentea, A. alba* (*Clematissa alba=A. nuttingi*) and *A. macrocalyx,* and two new species are described*; V. eminens* and *V. nyahae*. In addition, *Anthothela parviflora* has been reassigned to a new genus *Williamsius* so is now *Williamsius parviflora*, new combination. Finally, *Lateothela anitorkilda* n. gen., n. sp. has been proposed to accommodate a species that has historically been mistaken for *Anthothela grandiflora.*

2.5.1 Phylogenetically informative characteristics at the genus level

Morphological characteristics historically used to define *Anthothela* were found to be variously useful, with some characteristics demonstrating congruence with molecular groupings while others did not. This study has found the form of the sclerites present in the tentacles is an under-utilised taxonomically informative character, while polyp distribution or the degree to which a polyp is retracted is of little importance. Some of the colonies examined consisted of only tiny fragments so the utility of growth form as an informative characteristic at a species level has been difficult to assess. Nevertheless, growth form appears significant in defining the genus (if not the species). The configuration of the medulla, especially the arrangement of coelenteric canals within and surrounding has been, and remains, a significant morphological factor in defining the family Anthothelidae and to some degree, the genera within.

2.5.1.1 Medulla configuration

The presence of boundary canals is defined as a familial trait, but the Anthothelidae is considered "highly polyphyletic" (McFadden et al. 2010) so an assessment of the exact configuration of the boundary and internal canals at a genus level is potentially informative. Here, specimens found to have a large boundary space consisting of frequently anastomosing canals were assigned to *Victorgorgia* while *Anthothela*, *Lateothela* n. gen. and *Williamsius* n. gen. have clearly defined boundary canals which run parallel and rarely anastomose. Additionally, *Victorgorgia* has large, well-defined canals running longitudinally through the centre of the medulla throughout the colony while *Anthothela, Lateothela* n. gen. and *Williamsius* n. gen. have no or only very poorly defined central canals. Of the three genera for which molecular results were obtained, *Victorgorgia* was found to be significantly genetically distant from *Anthothela* and *Lateothela* n. gen. Thus the form and arrangement of the boundary and central medulla canals can be informative but only to distinguish distant genera. In fact, *Victorgorgia* differs enough, morphologically and genetically, from *Anthothela* to be in a different family; however until there is a major revision of the family Anthothelidae they remain together.

2.5.1.2 Polyp retractability and calyces

Historically, the ability of a polyp to retract entirely into a calyx was a characteristic used to define *Anthothela* (Broch 1912b; Grieg 1894; Verrill 1879a). After viewing many specimens, it is clear the polyps of *Anthothela* specimens can retract fully into a calyx but do not always do so thus it is not a useful generic character. Nevertheless, the presence of a calyx into which the polyp can retract remains an important characteristic for *Anthothela* (e.g. morphological differentiation between a membranous colony of *Anthothela* and *Anthelia fallax* depends in part on the presence or absence of a calyx).

2.5.1.3 Colony form

Historically, little emphasis has been placed on colony form to define *Anthothela,* with three possible colony forms eventually being described in the literature all apparently attributable to the genus (Sars 1856; Stiasny 1937; Studer 1894). Those three colony forms described match the colony forms of three of the genera assessed here, *Anthothela, Victorgorgia* and *Lateothela* n. gen. The colony form of *Williamsius* n. gen. is based on only a single colony examined (and descriptions of additional colonies in the literature) making characteristic colony form an as yet unconfirmed predictor for the genus but it is possible that future samples will allow such a distinction. It appears gross colonial form can be useful for generic distinction but any generalisations on colony form should be based on numerous observations and substantive colonies.

2.5.1.4 Colour

An additional morphological characteristic which could be considered informative is colour. Of the species in the genus *Victorgorgia* which have the live colour recorded, all are variations of vivid purple, magenta or mauve. Thomson (1927) published a description and superb figures of colonies of *A. grandiflora* collected off the coast of Portugal and Spain. Three colonies are portrayed in the figures as cream to yellow and one colony as purple. There is a possibility that this purple specimen is actually a specimen of *Victorgorgia*. Considering the increasing use of non-destructive photographic sampling of deep-water coral communities, striking colour differences could be very useful for diversity assessments. However, considering three of the known *Victorgorgia* species do not have live colour recorded, colour difference alone cannot facilitate reliable identification. Fresh *Anthothela* and *Lateothela* n. gen. specimens have only ever been recorded as pale yellow to creamy pink, thus these two genera cannot be reliably separated on colour.

2.5.1.5 Sclerites

The most reliable morphological diagnostic features for each of these genera are the shape and arrangement of the sclerites in the pinnules and tentacle rachis. Historically, these features were often completely overlooked or described only with simple generalisations. This diagnostic is an extremely useful morphological tool as even the smallest sample will usually have a tentacle that can be examined, no major dissection of a colony is necessary and membranous colonies of *Anthothela* or *Lateothela* n. gen. can potentially be identified without the presence of a medulla. The investigation of pinnule and tentacle sclerites in other genera in Anthothelidae may prove systematically informative.

2.5.2 Genetic distances and species delineation

Unfortunately, species delineation within the genera was not straightforward with minimal consistent morphological differences and often very little molecular variation. All intrageneric genetic distances using the concatenated gene regions were <0.018 (or 1.8%). In fact, within *Anthothela,* identical sequences across both gene regions were found for *A. grandiflora* and *A. vickersi* and within the genus all species differed by <0.007 (or 0.7%). McFadden et al. (2010) insisted that genetic distance of <1% (<0.01) does not preclude the possible presence of different species and suggest that genetic distances of >0.5% are “likely to be indicative of species-level differences”. Indeed more recently, an average genetic distance threshold of 0.3% was found to be the level at which the greatest number of species could be distinguished within *Alcyonium* whilst still minimising the false splitting of species units (McFadden, Brown, et al. 2014). In both papers the authors emphasise that these gene regions are “imperfect” but encourage their use as any power in species delineation using these gene regions increases with sample size and spread. Confident species assignations based on single nucleotide differences (or character-based methods) are a promising possibility, but require a greater understanding of intraspecific variability which is only possible in well-sampled populations and species (McFadden, Brown, et al. 2014). Unfortunately, comprehensive sampling of deep-water fauna is often impossible and singletons are common. Thus combining molecular, morphological and geographical results is currently the most effective approach to systematics of deep-water fauna.

Cairns & Baco (2007) similarly found low interspecific genetic distances in the genus *Narella* (<1.39% for mtMutS and <0.328% for ND6). In fact, three of the *Narella* species had identical sequences for both gene regions. Nevertheless the species were retained on the basis of morphological and geographical differences and the possibility was that the two gene regions used were of insufficient variation to allow full resolution at a species level. Similarly, Cairns & Bayer (2005) found that 13 sequences from *Primnoa* specimens were all identical using the mtMutS gene region. Again, they retained four species based on the morphological and geographical differences.

Despite the two gene regions used in the current study being both mitochondrial and highly conserved (Bilewitch & Degnan 2011; France & Hoover 2002; McFadden et al. 2011), delimiting *Anthothela* species based on distinct morphological and geographic separation, despite identical mitochondrial sequences, is defendable. Regardless, identical sequences between morphologically differing specimens from Norway and southern Tasmania are unexpected. A phylogeographic study on the wide-spread, deep-sea octocoral, *Paragorgia arborea* found a similar connection with specimens from the waters around New Zealand, eastern USA and Canada, and Norway sharing a haplotype consisting of six combined mitochondrial gene regions (including mtMutS and COI) (Herrera et al. 2012). They argue this haplotype (and others) are from one species unit, and that the species originated in the north Pacific Ocean, spread south into the south Pacific, then east possibly with the Antarctic Circumpolar Current, and then north into the western Atlantic Ocean. This evolutionary pattern is a plausible explanation for the seeming close relationship, both morphologically and genetically, between *A. grandiflora* in the north Atlantic and *A. vickersi* in the south Pacific. However, in this case the morphological differences in sclerites between *A. grandiflora* and *A. vickersi* are comparable to differences traditionally used in octocoral morphological taxonomy for species delineation (Fabricius & Alderslade 2001) and are therefore considered sufficient for species level separation. Thus, the origins and spread of *Anthothela* may concur with those found in *P. arborea* but possibly local conditions or differences in life history characteristics have led to a morphological divergence between the populations of *Anthothela*. However, this current study lacks information on haplotypes from the intervening waters (southern Atlantic or southern Pacific) and the gene regions used may be insufficiently variable for species-level phylogenies within *Anthothela*. Another *Anthothela* species here recorded in the Gulf of Mexico, *A. quattriniae* n. sp., has diverged genetically as well as demonstrating substantial morphological differences from the *A. grandiflora*/*A. vickersi* lineage even though it is geographically between these two species. It is possible niche ecological conditions within the limited boundaries of the Gulf of Mexico have influenced this divergence (Quattrini et al. 2013).

2.5.3 Phylogenetic relationships among *Anthothela*, *Lateothela* n. gen. and nominal *Alcyonium* species

The extended phylogenetic analysis indicates the family Anthothelidae is not valid and instead contains widely divergent genera, some of which are from different fundamental clades within the Octocorallia. The subfamily Anthothelinae is also highly polyphyletic and contains genera (*Anthothela* and *Lateothela* n. gen.) which are more closely aligned to *Alcyonium* (Alcyoniidae) than to other genera in the subfamily (e.g. *Victorgorgia* or *Alertigorgia*). *Alcyonium* is not only from a different family but is also from a different subordinal grouping.

Assuming these phylogenetic results might be reflected in the morphology, similarities in morphological characteristics between *Anthothela, Lateothela* n. gen. and *Alcyonium* can be sought. The difficultly arises that *Alcyonium* is probably polyphyletic as the northern hemisphere species have been shown to separate into four divergent clades (McFadden et al. 2011; McFadden et al. 2001). *Lateothela* n. gen. in particular is closely related to three of those (nominally *Alcyonium*) clades, and slightly more distantly related to the *Alcyonium digitatum* clade, which is assumedly the 'true' *Alcyonium.* It is more closely related to all these *Alcyonium* species than it is to the morphologically similar *Anthothela.* The current morphological grouping of *Alcyonium* is of fleshy, upright specimens which lack a true medulla but can also sometimes be encrusting only—distinctly different from the firm, distinct medulla present in *Lateothela* n. gen. However, there are significant similarities in sclerites between some *Alcyonium* species and *L. anitorkilda* n. gen., n. sp., if not in colony form. In Stokvis & van Ofwegen (2006), five encrusting *Alcyonium* species are described and figured. For some species (*A. grandiflorum* Tixier-Durivault & d'Hondt, 1974, *A. rubrum* spec. nov. and *A. profundum* spec. nov. in particular) the spiky josephinae clubs found in the tentacles are very similar to those of *L. anitorkilda* n. gen., n. sp. (compare Fig. 2a,b, Fig. 9b and Fig. 11b of Stokvis & van Ofwegen (2006) to Fig. 2.127 within). Additionally, some of the species have very similar sclerites to the short, stout, warty rodlets found in the calyces and cortex of *L. anitorkilda* n. gen., n. sp. (compare Fig. 3a,b of Stokvis & van Ofwegen (2006) to Fig. 2.129 within). In fact, a single mtMutS sequence from the specimen determined as *Alcyonium grandiflorum* in Stokvis & van Ofwegen (2006) falls within the *Lateothela* clade, however without an examination of the type specimen of *Alcyonium grandiflorum* and the additional gene region the exact relationship unfortunately remains unconfirmed. These similarities along with the intertwined molecular phylogeny with other *Alcyonium* species indicate a close relationship between *Lateothela* n. gen*.* and some nominal *Alcyonium* species but the presence of a medulla with boundary canals currently places *Lateothela* n. gen. in the Anthothelidae. Given the results within perhaps new familial groupings should be defined on sclerite type and arrangement and molecular clades rather than medulla or colony form. The genetic distance between genera with boundary canals suggests this morphological trait has evolved more than once.

In further evidence of the phylogenetic importance of sclerite form, *Alcyonium varum,* which here grouped very closely to the *Anthothela* group, has very similar sclerites to this genus. In particular, it has the spatulate clubs in the tentacles common in *Anthothela* (compare Fig. 9c in van Ofwegen et al. (2007) to Fig. 2.5B within). However, the colony form of *A. varum* is quite different to the other species of *Anthothela* and has been collected from sites considered too shallow for *Anthothela* specimens (albeit in Chilean fjords which may experience deepwater emergence). It may eventuate that *A. varum* is considered a membranous form of *Anthothela* or that the colony can develop branches with a medulla. An investigation of sclerite forms from the tentacles of *A. haddoni* and related species may also assist in defining their relationship with *Anthothela.*

2.5.4 Membranous species

It is possible some of the many encrusting species with similar polyp forms are membranous versions of *Anthothela* yet it is outside the scope of this project to entirely revise all suspected or possible species. The presence of branches with a medulla separated from the cortex by a ring of boundary canals, the lack of a single central stem, common anastomoses, the presence of a calyx and tuberculate spindles as the dominate sclerites type have historically been sufficient characteristics to place a specimen in *Anthothela,* but colonies without branches are much more difficult to confidently assign. A more robust designation of *Anthothela* herein with additional characteristics (specifically the presence of spatulate clubs in the tentacles and sclerites arranged longitudinally in the tentacle rachis) will hopefully assist future researchers to clarify some of the uncertainties with these membranous forms.

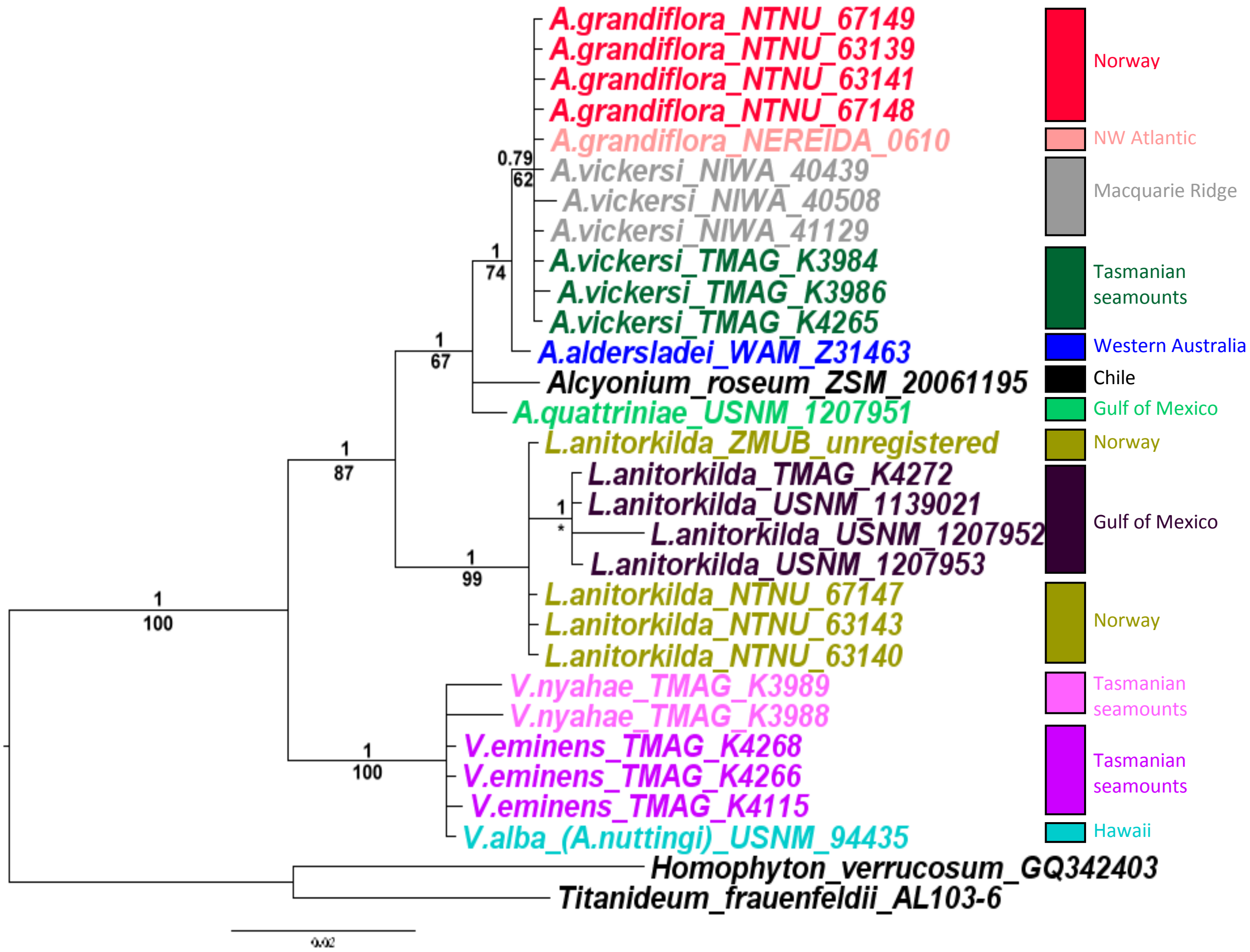
2.5.5 Summary

Those species and specimens historically assigned to the genus *Anthothela* were found to be from four different genera—a finding which was supported both morphologically and genetically. The family Anthothelidae and the subfamily Anthothelinae were found to be highly polyphyletic. Combining morphological and molecular approaches in this study, in general, proved effective and informative, especially at a genus level. However, conclusions at a species level were limited by small sample sizes and short gene sequences. The mitochondrial gene regions appear to be insufficiently variable for species delineation within *Anthothela* and possibly *Lateothela* n. gen. Many of the species descriptions here and historically are based on single (or very few) specimens and sometimes only a small piece of a single specimen as is the nature of deep-sea research. In these situations intraspecific morphological variation and geographic distribution are impossible to assess accurately. Nevertheless, this research reveals that the two genera, *Anthothela* and *Victorgorgia,* are found in both hemispheres and in the Atlantic, Pacific and Indian oceans, and *Lateothela* n. gen. is presently confined to the Atlantic Ocean. Collection depths of confirmed specimens indicate they are exclusively deep-water genera. There are undoubtedly further unrecorded species in poorly sampled areas of the oceans and there is likely to be significant diversity within these genera which has been overlooked in existing collections. Indeed, specimens of *L. anitorkilda* n. gen, n. sp. were found in every northern hemisphere collection searched for this study, almost always mistakenly determined as *A. grandiflora.*

Specimens from these genera are usually large, upright and somewhat fragile. These characteristics make these specimens relatively easy to spot in deep-water video surveys and thus to be used in biodiversity assessments but also mean they are at risk of damage from the impacts of fishing gear on the sea floor (Althaus et al. 2009). Untangling the taxonomy of the genus *Anthothela* will hopefully minimise incorrect identification of specimens and ensure biodiversity and fishing assessments can confidently utilise these often spectacular colonies.

2.6 Appendices

Appendix 1



Supplement Figure 1. Tree generated from the nucleotide sequence for the mitochondrial gene region, igr1–COI of *Anthothela*-like specimens. Bayesian posterior probabilities shown above branch, ML bootstrap values below branch; HKY+G (Bayesian results split freq = 0.0019, 10000000 gen, burnin=25000). (* indicates nodes present only in Bayesian analysis)

Appendix 2

Supplement Table 1. Taxa included in the extended phylogenetic analysis (Fig. 2.142) with voucher specimens and GenBank accession numbers (adapted from McFadden & van Ofwegen 2012c).

Taxa	Voucher	Igr1-COI	mutS
Acanthoaxis wirtzi	RMNH Coel.39502	JX203816	JX203764
Acanthogorgia breviflora	ZMTAU CO34194	GQ342378	GQ342464
Acrossota amboinensis	RMNH Coel. 40798	GQ342379	DQ985956
Acrophytum claviger	RMNH Coel.40222	JX203823	JX203770
Alcyonium acaule	BAN.AA1	GU355942	AY607775
Alcyonium bocagei	SAG.AC2	GU355943	GU355960
Alcyonium coralloides	RMNH Coel. 39678	GQ342380	GQ342465
Alcyonium digitatum	SBMNH 360700	GQ342381	GQ342466
Alcyonium glomeratum	GLE.AG23	GU355964	GU355947
Alcyonium glomeratum	LUZ.AG6	GU355948	AY607776
Alcyonium haddoni	ZSM 20061191	GU355958	GU355974
Alcyonium palmatum	RMNH Coel. 39685	GQ342382	GQ342467
Alcyonium spA (CSM)	IOM.BF.M2	GU355970	GU355955
Alcyonium varum (=*Alyconium roseum*)	ZSM 20061195	GQ342383	GQ342468
Alcyonium variabile	RMNH Coel. 40800	GQ342385	GQ342470
Anthomastus ritteri	RMNH Coel. 40802	JX203824	DQ302816
Cladiella sphaerophora	ZMTAU CO34132	GQ342386	GQ342471
Discophyton rudyi	CSM-DIRU15	GQ342387	DQ302808
Parasphaerasclera aurea	RMNH Coel.40799	JX203817	JX203766
Sphaerasclera flammicerebra	MNHN TER708.12	JX203818	JX203765
Parasphaerasclera aff. *grayi*	NTM-C014902 OR CO14092	JX203871	DQ302809
Parasphaerasclera rotifera	UF3890	GQ342388	GQ342472
Klyxum utinomii	ZMTAU CO34127	GQ342392	GQ342476
Lampophyton planiceps	RMNH Coel. 40201	GQ342393	GQ342477
Lobophytum pauciflorum	NTM-C014161	GQ342394	DQ280575
Malacacanthus capensis	RMNH Coel. 40801	GQ342395	DQ302811
Nephthyigorgia sp. CSM-2012	RMNH Coel.40819	JX203864	JX203804
Paraminabea aldersladei	NTM CO14895	JX203819	JX203767
Leptophyton benayahui	CSM-SAF361	GQ342434	GQ342507
Rhytisma fulvum	ZMTAU CO34124	GQ342396	GQ342478
Sarcophyton ehrenbergi	NTM CO14455	JX203821	DQ280516
Sarcophyton trocheliophorum	NTM CO14854	JX203822	JX203769
Sinularia querciformis	ZMTAU CO34096	GQ342399	FJ621469
Alertigorgia sp. CSM-2012	NTM CO14528	JX203825	JX203771
Diodogorgia nodulifera	RMNH Coel. 40803	JX203826	JX203772
Erythropodium caribaeorum	RMNH Coel. 40829	GQ342401	GQ342480
Titanideum frauenfeldii	AL103-6	GU563314	FJ264916
Homophyton verrucosum	RMNH Coel. 40805	GQ342403	GQ342482
Iciligorgia sp. CSM-2010	RMNH Coel. 40040	GQ342402	GQ342481
Ideogorgia capensis	RMNH Coel. 40804	GQ342428	GQ342502
Solenocaulon sp.	RMNH Coel. 40033	GQ342404	GQ342483
Anthothela nuttingi (=***Victorgorgia alba***)	USNM 94435	FJ264908	GU563313
Anthothela grandiflora	USNM 1014917		DQ297415
Arula petunia	RMNH Coel.40188	JX203827	JX203773
Briareum asbestinum	RMNH Coel. 40825	GQ342405	GQ342484
Stephanogorgia faulkneri	NTM CO14927	GQ342406	GQ342485

Trichogorgia capensis	RMNH Coel.40817	JX203863	JX203798
Azoria bayeri	RMNH Coel. 40806	GQ342407	GQ342486
Carijoa riisei	RMNH Coel.40807	JX203829	JX203775
Carijoa sp. 1 CSM-2012	RMNH Coel.40031	JX203832	JX203776
Cervera atlantica	RMNH Coel. 40838	JN620805	JN620804
Clavularia sp. CSM-2012	RMNH Coel.40809	JX203834	JX203778
Cryptophyton goddardi	RMNH Coel.40810	GQ342409	JX203779
Inconstantia exigua	RMNH Coel.40191	JX203870	JX203790
Inconstantia pannucea	RMNH Coel.40193	JX203841	JX203788
Inconstantia procera	USNM 1178386	JX203838	JX203782
Incrustatus comauensis	RMNH Coel. 33872	GQ342391	GQ342475
Knopia octocontacanalis	NTM CO15392	GQ342410	GQ342488
Paratelesto sp. CSM-2010	RMNH Coel. 40019	GQ342411	GQ342489
Phenganax parrini	CSM-NB2	GQ342412	GQ342490
Telestula sp.	NTM-C014984	JX203846	DQ302803
Telestula cf. spiculicola	OAS-28	FJ264917	GU563311
Trachythela rudis	REH221–1	FJ264909	GU563310
Coelogorgia palmosa	NTM CO14914	GQ342413	DQ302805
Cornularia pabloi	USNM 1178390	JX203847	JX203792
Actinoptilum molle	RMNH Coel. 40822	GQ342414	GQ342491
Dichotella gemmacea	NTM CO14929	GQ342415	GQ342492
Ellisella sp. 2 CSM-2012	RMNH Coel.40812	JX203850	JX203793
Viminella sp. 1 CSM-2012	RMNH Coel.40032	JX203852	JX203794
Eugorgia multifida	UABCS-013	GQ342417	GQ342494
Eunicella tricoronata	RMNH Coel.40814	JX203853	JX203795
Gorgonia flabellum	RMNH Coel. 40827	GQ342418	GQ342495
Leptogorgia rigida	UABCS-008	GQ342420	GQ342496
Pacifigorgia media	UABCS-015	GQ342421	GQ342497
Pinnigorgia flava	RMNH Coel. 40815	GQ342422	GQ342498
Pseudopterogorgia bipinnata	RMNH Coel. 40828	GQ342423	GQ342499
Pseudopterogorgia elisabethae	RMNH Coel.40831	JX203854	JX203796
Pterogorgia anceps	RMNH Coel. 40837	GQ342424	GQ342500
Rumphella sp. CSM-2012	RMNH Coel.40816	JX203855	JX203797
Halipteris finmarchica	NTM CO14596	GQ342425	DQ302868
Heliopora coerulea	CRCNI 577	GQ342426	DQ302872
Ifalukella yanii	UF4139	GQ342427	GQ342501
Melithaea erythraea	ZMTAU CO34216	GQ342430	GQ342503
Melithaea sp. 2 CSM-2012	RMNH Coel.40034	JX203857	JX203800
Wrightella coccinea	RMNH Coel. 40041	JX203858	JX203801
Dendronephthya sinaiensis	ZMTAU CO34163	GQ342433	GQ342506
Eunephthya thyrsoidea	RMNH Coel.40182	JX124384	JX124364
Gersemia rubiformis	CSM-C59	GQ342473	GQ342390
Gersemia juliepackardae	VEN3208-A3	JX203820	JX203768
Lemnalia sp. CSM-2012	RMNH Coel.40818	JX203859	JX203802
Nephthea elatensis	ZMTAU CO34112	GQ342435	GQ342508
Paralemnalia thyrsoides	ZMTAU CO34087	GQ342436	GQ342509
Scleronephthya corymbosa	ZMTAU CO34159	GQ342438	GQ342511
Stereonephthya cundabiluensis	ZMTAU CO34204	GQ342439	GQ342512
Chironephthya sp. CSM-2010	ZMTAU CO34203	GQ342440	GQ342513
Nidalia sp.	NTM-C014876	GQ342441	DQ302828
Pieterfaurea khoisaniana	CSM-SAF183	GQ342437	GQ342510
Siphonogorgia godeffroyi	RMNH Coel.40833	JX203860	JX203803
Ceeceenus quadrus	UF2858	GQ342442	GQ342514

Paralcyonium spinulosum	RMNH Coel. 40820	JX124389	DQ302833
Studeriotes sp. CSM-2010	RMNH Coel. 40043	GQ342443	GQ342515
Astrogorgia sp. CSM-2012	RMNH Coel.40018	JX203861	JX203805
Bebryce sp. CSM-2012	RMNH Coel.40821	JX203862	JX203806
Eunicea tourneforti	RMNH Coel. 40835	GQ342445	GQ342517
Euplexaura sp. CSM-2010	ZMTAU CO34220	GQ342446	GQ342518
Menella sp. CSM-2010	RMNH Coel. 40038	GQ342447	GQ342519
Muricea atlantica	RMNH Coel. 40834	GQ342448	GQ342520
Muriceopsis flavida	RMNH Coel. 40830	GQ342449	GQ342521
Plexaura kuna	RMNH Coel.40836	JX203866	JX203807
Plexaurella nutans	RMNH Coel. 40826	GQ342451	GQ342523
Pseudoplexaura wagenaari	RMNH Coel. 40832	GQ342452	GQ342524
Callogorgia formosa	NTM CO14593	GQ342453	GQ342525
Thouarella grasshoffi	USNM 1078188	FJ268636	GQ868334
Renilla sp. CSM-2010	UF4000	GQ342455	GQ342526
Annella mollis	NTM CO14924	GQ342456	JX203808
Subergorgia suberosa	NTM C014930	GQ342457	JX203809
Taiaroa tauhou	NIWA 28679	JX203867	JX203810
Tubipora sp. CSM-2012	ZMTAU CO34116	GQ342458	JX203811
Virgularia schultzei	RMNH Coel. 40823	GQ342459	GQ342527
Anthelia glauca	ZMTAU CO34183	GQ342460	JX203812
Asterospicularia randalli	UF2851	GQ342461	DQ302836
Cespitularia erecta	OCDN-8504C	JX203869	JX203813
Heteroxenia fuscescens	ZMTAU CO34118	GQ342462	GQ342528
Sarcothelia edmondsoni	CSM-SKB	JX203868	JX203814
Sympodium caeruleum	ZMTAU CO34185	GU356009	JX203815
Xenia hicksoni	ZMTAU CO34072	GQ342463	GQ342529

Chapter 3. A taxonomic revision of the genus *Primnoisis* (Alcyonacea: Isididae) using morphological and molecular data.

3.1 Introduction

3.1.1 Systematic position of *Primnoisis* Studer [& Wright], 1887

The genus *Primnoisis* is in the family Isididae, part of the suborder Calcaxonia and within the order Alcyonacea. Isididae is a well-recognised family of octocorals with colonies of articulated axes consisting of alternating proteinaceous nodes and calcareous internodes, commonly known as 'bamboo coral'. The family contains approximately forty described genera grouped into four subfamilies, established on colony and branching form and dominant sclerite type. There is some phylogenetic evidence that the subfamilies are sufficiently divergent to be given full family status including a novel mitochondrial gene arrangement in the subfamily Keratoisidinae (Brockman & McFadden 2012; Brugler & France 2008)

Within the subfamily Mopseinae Gray, 1870, *Primnoisis* has been recognised as a relatively well-established and stable genus for a number of years (Alderslade 1998). However, within the genus the recognition and identification of the described species has been problematic and confusion regarding informative and reliable morphological characteristics remains.

Currently there are 8 recognised species of *Primnoisis; P. antarctica* Wright & Studer, 1889; *P. sparsa* Wright & Studer, 1889; *P. ambigua* Wright & Studer, 1889; *P. rigida* Wright & Studer, 1889; *P. delicatula* Hickson, 1907; *P. fragilis* Kükenthal, 1912; *P. formosa* Gravier, 1913 and *P. mimas* Bayer & Stefani, 1987b.

3.1.2 The establishment of the genus

A small fragment of decorticated isidid skeleton collected northwest of Îles Kerguelen in the southern Indian Ocean during an expedition on the SMS *Gazelle* was described by Studer (1878) and given the name *Isis antarctica* n. sp. The specimen was described as 14cm tall with a single main axis and branches emanating only from the internodes. Each internode was described as having 3–4 fine, transverse branches arising at different heights and these branches quickly divided into even finer twigs. The bottlebrush branching architecture of this damaged specimen was sufficiently different from previously recognised species of Isididae for Studer to erect a new species, however he admitted that without any polyps or sclerites it was impossible to confidently assign the sample to a genus. He suggested *Isis*, or his new genus *Sclerisis* as an alternative, based only on the branching mode of the colony.

Studer (1887), in collaboration with E.P. Wright, published a description of a new genus *Primnoisis* and a new subfamily Primnoisidinae based on specimens collected during the HMS *Challenger* expedition which had the same distinctive bottlebrush branching architecture as the *Isis antarctica* specimen. One specimen, collected near Prince Edward Island, was designated as *Primnoisis antarctica* and is now recognised as the specimen on which the characters of the genus are based rather than the denuded nominal type specimen of *Isis antarctica* (Alderslade 1998; Bayer & Stefani 1987b).

There exists some confusion as to the correct authorship of *Primnoisis*, as the paper where it is first mentioned was published by Studer in 1887. But in that paper he briefly mentioned it was written in collaboration with Wright and the authors of the genus are stated as Wright and Studer, perhaps presupposing the publication of the HMS *Challenger* report with its more substantial description of the genus based on the *Challenger* specimen (Wright & Studer 1889). However, in the *Challenger* report, on page xlv, the authorship of *Primnoisis* is listed as "Wright and Studer, Archiv f. Naturgesch., Jahrg. liii. Bd. i. p. 46, 1887", which is a clear reference to the Studer (1887) paper, suggesting the researchers intended the author to be Wright & Studer, 1887, despite this first appearance being in a paper authored by Studer. To add to the confusion, the *Challenger* report has *Primnoisis* "new genus" in three separate places (Wright & Studer 1889) despite the genus having already been established in the earlier paper. Regardless, as the first mention of the genus was in the Studer (1887) paper with Wright's approval, the consensus appears to be that the genus *Primnoisis* should be attributed to Studer [& Wright], 1887 (Alderslade 1998; Bayer & Stefani 1987b).

Studer [& Wright] (1887) erected the new subfamily Primnoisidinae to encompass isidid specimens which have many branches arising from the internodes, have "becher-, keulenförmig oder cylindrisch " polyps (cup-, club-shaped or cylindrical) with non-retractile tentacles which close over the polyp mouth and have relatively large sclerites which are curved plates or scales with interlocking toothed edges, on both the polyps and in the coenenchyme. Significantly, they specified that, for the whole subfamily, the sclerites in the tentacles "bilden sie in der Regel drei Längsreihen" (usually arranged in three longitudinal rows). This appears to be a reference to a longitudinal arrangement of multiple sclerites on the polyp summit. The protective structure at the polyp summit, here referred to as the anthopoma or anthopomal region, is formed by those sclerites "on and just below the base of the tentacles" (Alderslade 1998) and consists of eight triangular sectors called octants. The presence and arrangement of a compound group of longitudinal sclerites in the anthopoma later became a source of some confusion but eventually became one of the defining characteristics of *Primnoisis* (Alderslade 1998).

Studer [& Wright] (1887) included three genera in the subfamily Primnoisidinae; *Primnoisis*, *Mopsea* Lamouroux 1816 and *Acanthoisis* Wright and Studer 1889. However this subfamily was not adopted by later authors, as Gray had previously established the subfamily Mopseadae (=Mopseinae) in 1870 (Alderslade 1998; Wright & Studer 1889).

Primnoisis is originally described as an isidid with alternating internodes and nodes, branching from the internodes in many planes and with large polyp scales (Studer & [Wright 1887). The expanded definition in Wright & Studer (1889) included the colonies from the HMS *Challenger* expedition which were abundantly branched with all branches originating from the internodes, in all planes and branching up to the fifth degree, with usually 3-4 branches per internode such that the colony formed a thick bush. They suggested a “loose to close spiral” arrangement of the “club- or cup-shaped” polyps, at right angles or angled upwards towards the apex of the twig. They also stated that “in the tentacles two to three rows of scales form the skeleton”—it is not clear if they were referring to actual tentacle sclerites or if they were describing the anthopomal sclerites, which they mistakenly were presuming were on the back of the tentacles. The internodes were described as covered with a thin coenenchyme consisting of “flattened, longish, lancet, rod-like or irregular scale-like bodies covered with warts or spines”, interlocked by the edge serrations (Wright & Studer 1889). However, in this expanded genus definition they also introduced three characteristics which have not persisted as generic characteristics. One of these was that the polyps were arranged in spirals. Many subsequent researchers searched in vain for polyps arranged in spirals in *Primnoisis* colonies and eventually it was abandoned as a consistent characteristic of the genus (Gravier 1914; Hickson 1907; Kükenthal 1912). An additional characteristic was first mentioned in Studer [& Wright] (1887) as “…die Mesenterialfalten mit kleinen Kalkspicula erfüllt” (the mesenteric folds are filled with small calcium spicules). This characteristic is not mentioned by subsequent researchers (Alderslade 1998; Bayer & Stefani 1987b; Hickson 1907; Kükenthal 1919) although Wright & Studer (1889) repeated the character description with “mesenterial folds are in great part so filled with calcareous spicules that these remain well preserved and rigid” and describing the sclerites as “very small, calcareous rodlets”.

Finally, Wright & Studer (1889) described two layers of different sclerites for the polyps but the details of this arrangement are not clear in their text—“in the polyps there is a deep layer of rod-like indented scales, which are placed in eight longitudinal rows and surround the periphery like so many chains; above these are flat, transversely placed scales, with toothed edges and warty or thorny surfaces whose edges interlock” (Wright & Studer 1889). This characteristic of two layers of sclerites was also mentioned by Kükenthal (1919) but has not persevered in subsequent descriptions. Wright & Studer (1889) mentioned it in the genus description and in one species description only (*P. rigida*).

Wright & Studer also noted the similarities of the new isidid genus with *Dasygorgia* (Chrysogorgidae), defining the resemblance as the "scaly" nature of the sclerites, the lower layer of calcareous rods and the condition of the tentacles folding over the polyp mouth (Wright & Studer 1889). They emphasised the similarities multiple times, including in the discussion of the sub-family Chrysogorginae (Wright & Studer 1889). Any resemblance to primnoids (as suggested by the genus name) is mentioned as "superficial" and relating only to the shape of the polyps.

3.1.3 The addition of other species

Four species of *Primnoisis* were described by Wright & Studer (1889), all based on specimens collected during the HMS *Challenger* expedition. The first, *Primnoisis antarctica,* has become the specimen on which the genus characteristics are based as mentioned above, and the three other species were *P. sparsa, P. rigida* and *P. ambigua*. *P. sparsa* was separated from *P. antarctica* based on branching which was more sparse, the more "rough and spiny" polyp body sclerites and the "form of the polyps" although what is different in the form of the polyps was not explicitly stated nor immediately obvious from the descriptions (Wright & Studer 1889). They described *P. rigida* as very bushy with branching to the fifth order, few nodes in the distal branches and small, acutely angled polyps with "eight regular vertical rows" of body sclerites (Wright & Studer 1889). *P. ambigua* was also described as bushy but with the branches predominantly branching in one plane and the polyp and coenenchyme sclerites as very "prickly" (Wright & Studer 1889). A complex anthopomal arrangement was mentioned for *P. antarctica, P. sparsa* and *P. rigida* but not for *P. ambigua* (Alderslade 1998; Wright & Studer 1889). Other than *P. antarctica,* the species erected by Wright & Studer (1889) have not been extensively reviewed. The original descriptions were relatively lengthy but lack comprehensive drawings or details of the arrangement of the polyp sclerites thus few researchers have been able to confidently assign specimens to these species.

In subsequent years more species were added to *Primnoisis,* based chiefly on branching and colony form, that is, dense bottlebrush or bushy growth forms of isidids; but the shape and ornamentation of the sclerites on the polyps and specifically the arrangement of the anthopoma were yet to be recognised as significant so were rarely adequately described or, in some cases, incorrectly described.

In a confusing contribution, Hickson (1907) reviewed isidid specimens which he assigned to a genus he erroneously called *Ceratoisis,* but which was recognised by other researchers as *Keratoisis* Wright, 1869. While describing two new Isididae species, Hickson decided that the distinction between *Ceratoisis* and *Primnoisis* was insufficient to warrant maintaining *Primnoisis* as a valid genus. One of the new species he described was C*eratoisis spicata,* which was subsequently transferred to *Primnoisis* by Kükenthal (1919) and finally became the type species for a new genus *Echinisis* Thomson & Rennet, 1931. The confusion arose from the presence of spines projecting above the polyp in *C. spicata* as in other *Keratoisis* species yet *C. spicata* had a bushy growth form closer to *Primnoisis* (Hickson 1907; Nutting 1910). Hickson argued that maintaining the distinction between *Keratoisis* and *Primnoisis* was unsustainable with *C. spicata* as the link between the genera. He suggested *Primnoisis* be synonymised with *Ceratoisis* (=*Keratoisis*), however subsequent authors did not agree and *Primnoisis* was retained (Grant 1976; Kükenthal 1912; 1915; 1919; Nutting 1910). Additionally, Hickson (1907) described another species, *Ceratoisis (Primnoisis) delicatula* which has remained as a valid *Primnoisis* species despite some doubts (Bayer & Stefani 1987b) [but see (Alderslade 1998)]. Hickson described the C*eratoisis (Primnoisis) delicatula* colony as a "tangled mass" with "no main stems" and with fine delicate branches. He also determined two other colonies as *Ceratoisis (Primnoisis) antarctica* although this determination was questionable as he declared the "scales on the back of the tentacles are all horizontally placed" and depicted this in a diagram (Hickson 1907 Pt II, fig 15). He may have been referring to transversely placed tentacle sclerites but the specification of the back of the tentacles suggests he was probably describing anthopomal sclerites. This description of horizontally placed sclerites on the back of the tentacles reappears in other literature (Kükenthal 1912; 1919) despite Studer [& Wright] (1887) stating that there were three longitudinal rows in the original genus description. In fact, Bayer & Stefani (1987b) stated that "the drawings given by Kükenthal (1912: 340, figs. 55-57) are sufficient to demonstrate that his specimen probably was not the species taken by the *Challenger*". Multiple, longitudinally placed anthopomal sclerites later becomes one of the defining characteristics of *Primnoisis* (Alderslade 1998) and specimens with horizontally placed anthopomal sclerites are now excluded from the genus.

Two specimens collected during the Deutschen Sudpolar-expedition of 1901 were described by Kükenthal (1912) as the new species *Primnoisis fragilis*. These specimens were distinguished from existing *Primnoisis* species on the basis of having very little secondary branching, crowded polyps and the lack of clear rows of polyp body sclerites.

Soon afterwards Gravier (1913) published a description of another *Primnoisis* species, *P. formosa,* based on specimens collected during the Deuxieme Expd Antarctique Francaise in 1908–1910. A more extensive description with drawings and photographs was published in the full expedition report (Gravier 1914). Gravier claimed *P. formosa* to be clearly distinguishable from the existing *Primnoisis* species but failed to explain this opinion. In fact, although Gravier's description is basically adequate, it is not clear why this colony is sufficiently different from others to warrant erecting another species (Bayer & Stefani 1987b; Grant 1976; Kükenthal 1919). Later, Molander (1929) assigned fresh specimens to *P. formosa* and stated that this species of Gravier differs from *P. delicatula* and *P. ambigua* mainly by the short length of the axis internodes.

The history and current situation of *Primnoisis* was summarised by Bayer & Stefani (1987b) who reassigned a number of species to other Isididae genera (see below). In that paper, some specimens collected near South Georgia in 1966 and 1976 were described with substantially different sclerites shapes and colony form; enough to justify the establishment of another *Primnoisis* species despite the confusion over the existing species. *Primnoisis mimas* was described as being “stouter and more robust” and the polyp body sclerites were “more deeply and sharply serrated, and smaller” than previously described species. However, the concession was made that an “intensive study of more abundant material” is required before confident and reliable identifications can be made (Bayer & Stefani 1987b).

3.1.4 Incorrectly assigned species

As mentioned, a number of other species have been erroneously assigned to *Primnoisis* and later reassigned to other genera.

In the same paper in which *Isis antarctica* was first described, Studer (1878) also established a new genus *Sclerisis* with *S. pulchella* as the type species. In the first part of his seminal work Kükenthal, (1919) withheld *Sclerisis* from the “system” and only included it as an uncertain genus, on the basis that the genus was described from one small fragment of a colony and had not been found since. However, in the second part of the same work, Kükenthal (page 927) appeared to re-examine the type specimen and declared *S. pulchella* to be a species of *Primnoisis* despite the often forked slender spindles found on the polyp body. Later, however, based on new material, Bayer & Stefani (1987a) re-established the genus *Sclerisis,* confirmed *S. pulchella* as the type species and added a new species, *S. macquariana*.

A preliminary list of Alcyonaria collected on the R.I.M.S Ship *Investigator* in the Indian Ocean by Thomson & Henderson (1905) mentioned *Primnoisis alba* n. sp. with a brief description . However, a year later the same authors (1906) published a full account of the collection from the expedition including some corrections, where *Primnoisis alba* is mentioned as “a misinterpretation” and the authors asked for the species to be “delete(d)”, although no specific reasons were supplied. Given the location from where the specimen was collected (Andamans, northern Indian Ocean) it is highly unlikely this specimen is *Primnoisis*. The type specimen has not been traced.

Other specimens temporarily assigned to *Primnoisis* include *Ceratoisis ramosa* Hickson, 1904, moved to *Primnoisis* by Kükenthal (1919) and finally to *Chathamisis* by Bayer & Stefani,(1987b). A denuded specimen assigned to the name *P. ramosa* by Thomson & Ritchie (1906) (independent of the Hickson species) and additional specimens from Roule (1908) were excluded by Kükenthal (1919) as insufficiently described. Additionally, the Thomson & Ritchie specimen is excluded from *Chathamisis ramosa* by Bayer & Stefani (1987b), presumably as it is impossible to confirm the identification without any polyps or sclerites.

As mentioned above Hickson (1907), while arguing for *Primnoisis* to be subsumed into *Ceratoisis* (= *Keratoisis*), described a species *Ceratoisis spicata*. Nutting (1910) declared that this specimen showed no indication of the true spindles present in *Keratoisis* Wright, 1869 and therefore transferred it to *Primnoisis.* This specimen was later designated as the type specimen for the new genus *Echinisis* Thomson & Rennet, 1931. A species erected by Kükenthal (1912), *Primnoisis armata,* was also reassigned to *Echinisis* by Thomson & Rennet (1931) but Bayer & Stefani (1987b) expressed reservations regarding the validity of the species due to similarities with *E. spicata*.

Deichman (1936) described *Primnoisis humilis* which was subsequently designated as the type species for *Stenisis* Bayer & Stefani, 1987b.

A specimen collected from the Cape of Good Hope and described as *Isidella capensis* by Studer (1878), was mentioned as *Primnoisis* (*Isidella*) *capensis* by Wright & Studer (1889) but only in the distribution of the genus *Primnoisis,* and then transferred to *Chelidonisis capensis* by Kükenthal (1919). Figures of the sclerites from Studer's type specimen in Stiasny (1941) convinced Bayer & Stefani (1987b) that Kükenthal had been wrong to place the species in *Chelidonisis* and they suggested it may be a melithaeid but this has not been clearly established. Hickson (1900) described a different specimen as *Primnoisis capensis* (Studer) but later claimed it was "closely related to, if not identical to" *Wrightella coccinea* (Hickson 1904), and Bayer & Stefani (1987b) also suggested it is a melithaeid. It is not clear exactly where these specimens belong but there appears a consensus that they do not belong in *Primnoisis.*

3.1.5 The need for a review

There were a number of years where colonies of *Primnoisis* continued to be collected and assigned to described species but often with some reservation (Branch & Williams 1993; Deichmann 1936; Eguchi 1964; Grant 1976; Gutt & Piepenburg 2003; Pasternak 1993; Sánchez & Rowden 2006; J. A. Thomson & Rennet 1931). Wright & Studer (1889) defined the distribution of the genus as "essentially Antarctic" while including the collection of *P. rigida* off Rio de la Plata at a latitude of 37^{o} south. Subsequent collections confirmed this general Antarctic distribution with the specimen of

P. rigida remaining an anomaly. The present study demonstrates that *Primnoisis* appears to be restricted to the Southern Ocean but not strictly Antarctic waters with many records north of 40^{o} south. Specimens of *Primnoisis* have been recorded from sites spread right round the Antarctic continent thus suggesting a circumpolar distribution for the genus. However, the distribution of particular species is more difficult to ascertain due to the unreliability of the taxonomy.

The most recent attempt at clarification of the genus by Alderslade (1998), addressed the generic description and highlighted the need for revision of the established species. The argument was made that the complex nature of the anthopoma may be unique to *Primnoisis.* Many small, warty, flat rods and occasionally asymmetrical triangles are arranged longitudinally to obliquely forming an interlocked compound octant. The transversely arranged body scales merge with each octant in a continuous manner and give the appearance that this transverse arrangement of the body sclerites continues into the anthopoma perhaps contributing to the misunderstanding and the seemingly incorrect interpretation of the anthopomal arrangement seen in Hickson (1907) and Kükenthal (1912). Alderslade (1998) stated that the type specimen of *Mopsea gracilis* Gravier, 1913 also has this complex anthopomal arrangement and thus may in fact be a specimen of *Primnoisis.*

The need for a review of the genus *Primnoisis* has become increasingly necessary with more frequent collecting expeditions in the Southern Ocean and the development of equipment which allows easier access to deeper waters but this has resulted in a greatly increased number of specimens which are unable to be assigned to a species. Some bushy isidid specimens brought to the surface from cold southern waters can be relatively confidently assigned to *Primnoisis,* but with only the original descriptions to work from it is impossible to confidently assign these specimens to any existing species or to identify any undescribed species. Recent work around the Antarctic Peninsula suggests that *Primnoisis* may be an early colonizer, quickly establishing colonies in disturbed areas after iceberg scour (Gili et al. 2001). It is neither immediately clear nor easy to clarify whether this is a characteristic specific to a particular species or the genus as a whole and whether it is consistent between geographical areas. Additionally, the assumption of circumpolar distribution, which has stood for many Antarctic species based on the hydrodynamics of the Antarctic continent, has more recently suffered some refutation. A number of different genera have been shown to include cryptic species with very narrow distributions (Baird et al. 2011; Hunter & Halanych 2010; Raguá-Gil et al. 2004; Wilson et al. 2007) but this is far from universal (Raupach et al. 2010). *Primnoisis* is a good candidate to contribute to this collation of distribution patterns as it is common, relatively easily recognised at a generic level and has been historically recorded all around the Antarctic continental shelf. However, without a full review of the existing species descriptions to elucidate the differences the question of cryptic species or circumpolar distribution cannot be effectively addressed.

3.1.6 Existing phylogenetic knowledge of *Primnoisis*

Very little phylogenetic research has been conducted on *Primnoisis* specimens to date. Some recent research has concentrated on relationships within the family Isidiae, particularly considering gene arrangement within the mitochondrial genome (Brugler & France 2008; van der Ham, Brugler, & France 2009). The subfamily Keratoisidinae has been shown to have a different mitochondrial gene arrangement to the other subfamilies within Isididae, including Mopseinae and within that specifically *Primnoisis* (Brugler & France 2008) which appears to have the most common octocoral gene arrangement in the mitochondrial genome.

3.1.7 Aims and summary

The taxonomic confusion within the genus *Primnoisis* largely stems from original descriptions which do not allow confident species assignation due to a lack of reliable or agreed characteristics for species delineation. Additionally, collection of *Primnoisis* specimens has been haphazard and opportunistic thus restricting any geographical or depth analysis, and no molecular results exist which could assist with species assessments.

This paper aims to review and clarify the taxonomic status, definition and range of the species within *Primnoisis* by combining morphological and molecular data. All nominal described species are reviewed and morphologically redescribed from the type specimens. Specimens collected in recent voyages to Antarctica, southern Australia and New Zealand seamounts, Macquarie Island and Heard Island are included in the review. A molecular phylogenetic analysis conducted on these recent specimens aims to facilitate a dual approach to the review and also assist in defining phylogenetically informative morphological features which correspond to genetic clades.

As a result, six of the seven nominal species have been retained in *Primnoisis,* one species has been synonymised, *Mopsea gracilis* Gravier, 1913 has been re-assigned to the genus and five new species have been added.

3.2 Material and Methods

3.2.1 Samples

Type specimens of the nominal species were obtained from the National Museum of History (NMHUK), Muséum national d'Histoire naturelle (MNHN), Museum für Naturkunde (ZMB) and National Museum of Natural History (NMNH).

Samples were sourced from many institutions and a variety of research voyages in the Southern Ocean south of Australia plus one voyage around the Scotia Arc. A significant number of samples were collected by CSIRO Marine and Atmospheric Research (CMAR) aboard the RV *Southern Surveyor* (SS) as part of a decadal study (1997 and 2007) of the seamounts south of Tasmania, Australia. These samples were all photographed on deck and preserved in 70% alcohol. Further samples from this area were obtained by CSIRO in 2008/09, collected using the remotely operated vehicle JASON aboard the RV *Thomas G. Thompson* (TT). These samples were photographed in situ and frozen once aboard the vessel. A number of samples, obtained from the Australian Antarctic Division (AAD), were collected for research during commercial fishing voyages to the Heard Island and MacDonald Island region (HIMI) in the southern Indian Ocean. The samples were collected aboard the FV *Southern Champion* (SC) on a number of different voyages and samples were frozen on board. Samples from one voyage (SC26; 2003) were defrosted, photographed, then preserved in 10% formalin mixed in seawater and transferred to 70% ethanol after a maximum of two months. Samples from subsequent voyages (SC46; 2008 and SC50; 2008), after defrosting, were preserved in 70% ethanol. Additional samples were obtained during the Collaborative East Antarctic Marine Census (CEAMARC) voyage aboard the RV *Aurora Australis* from the eastern Antarctic continent in 2007/08. These samples were photographed on board then preserved in 80% ethanol. Further samples were obtained from the National Institute of Water & Atmospheric Research (NIWA); chiefly from a research voyage to Macquarie Ridge, Macquarie Island south of New Zealand aboard the RV *Tangaroa* in 2008 and from a number of other voyages including to the Ross Sea, Antarctica and the seamounts east of New Zealand.

Fresh samples were collected on a research voyage aboard the RV *Aurora Australis* along the East Antarctic coastline between the Australian Antarctic bases Casey and Davis during the summer of 2009/10. The two targeted areas, known as Bruce Rise and Tressler Bank, are off the Shackleton Ice Shelf at approximately 63.1679°S; 101.7747°E and 65.0207°S; 94.2753°E respectively. Samples were collected by beam trawl with a 20 mm mesh net and were part of another research project into the implications of demersal fishing practices in the area. The trawling was conducted along transects running from the continental shelf (~500m) down the continental slope to depths of approximately 1200m. All trawls conducted had a video camera attached, recording the sampling event. Coral specimens were selectively removed from the bulk of the trawl contents as soon as possible, photographed and then placed in 100% ethanol. Preservation was ideally achieved within half an hour of specimens reaching the surface to minimise DNA degradation, a recognised problem for corals (Miller et al. 2010).

In addition, *Primnoisis* specimens were borrowed from the Australian Museum (AM), South Australian Museum (SAM), Northern Territory Museum and Art Gallery (MAGNT), Museum Victoria (MV) and the Tasmanian Museum and Art Gallery (TMAG). Registration numbers are used when available.

3.2.2 Morphological characters and methods

The key characteristics used to distinguish *Primnoisis* from other Mopseinae genera are the presence of a bushy colony, internodes with low longitudinal ridges but lacking spines or prickles, scale-like polyp body sclerites arranged transversely and a particular complex structure to the anthopoma (Alderslade 1998).

The **anthopoma** is the protective arrangement of sclerites covering the oral region of the polyps, and is “analogous but not homologous to the operculum”, a term often used for the same area in the Primnoidae (Alderslade 1998). Eight roughly triangular segments, placed between the mesenteries, extend from the polyp body to fold over the oral region. Each of these is known as an **octant** and together they comprise the anthopoma. In *Primnoisis*, each octant has a complex array of small, interlocked, irregularly shaped sclerites arranged longitudinally to obliquely. Tentacles extend from the tip of the octants and have transversely placed, crescent-shaped sclerites. In some Mopseinae genera, the polyps are tightly curved making the anthopoma asymmetrical due to reduced sclerites in the octants on the adaxial side (Alderslade 1998). *Primnoisis* polyps are not closely adherent to the axis and the anthopomas are considered symmetrical (although no octants are identical). Below the anthopoma, on the polyp body wall, sclerites are arranged transversely in irregular **series**—the number of series is determined by counting the number of sclerites discernible in a single line between the base of the polyp and the base of the anthopoma on the side of the polyp not closest to the branch (**abaxial** side).

Internodes, (the calcareous structure which alternates with the horny **nodes** in the axis of all Isididae) have **primary ridges** which run longitudinally virtually the whole length of the internodes and have “pronounced shoulders at each end” (Alderslade 1998).

Morphological characteristics of colonies were examined using the standard methods described in Alderslade (1998) and Fabricius and Alderslade (2001). Colonies were described for general shape, size and branching architecture. Whole colony photographs were taken, but varied in method and thus in quality as dictated by the situation. Those colonies examined in international museums were often photographed with constraints on time, facilities and equipment. Some colonies were photographed by the host museum and a small piece only was sent for examination.

Measurements taken included total height and breadth of colony where possible, length and width of internodes and nodes, branch angles, degrees of ramification, number of branches and polyps per internode, distance between polyps and polyp orientation. The length and width of polyps (up to 10 per colony if possible) were also recorded. Measurements were taken using a graticule under a dissecting microscope to the nearest half millimetre. If applicable, details of holdfasts and substrate were also noted.

Sclerites were sampled from four zones of the colonies: tentacles, anthopoma, polyp body and coenenchyme. In each case, a small piece of tissue was removed from the appropriate area and dissolved in a drop or two of liquid chlorine (bleach; 125 g/L available chlorine) on a microscope slide. Using a Leica DM1000 compound microscope, the dissolution process was usually observed and noted as this aided the process of confirming the positioning of the sclerites. To investigate if the arrangement of sclerites in the anthopoma was species-specific the anthopoma region was photographed and drawn. This process was occasionally facilitated by leaving the anthopoma overnight in a 2M solution of KOH to clear body tissue while leaving the sclerites in their original position, permitting much improved observation.

For the descriptive illustrations photographs of polyps and the colony surface were taken with a Leica MZ95 dissecting microscope using horizontal illumination and sclerite photographs were taken with a Leica DM2000 compound microscope. In both cases a Leica DFC420 camera was used to obtain image z-stacks manually as the microscope was focussed through the area of interest, and extended focus software (Combine Z: Alan Hadley) was used to merge the photographs into a single montage. For the purposes of general comparative taxonomy, sclerites were drawn using a Leica microscope drawing tube. All photographs were assembled into descriptive figures using Ulead PhotoImpact 12 image software.

A JEOL JSM-6701F Field Emission scanning electron microscope was used for electron micrographs of whole polyps and anthopomal arrangements. Small sections of twigs with a number of undamaged polyps were selected for mounting. To remove superficial surface tissue, each twig was then briefly immersed in approximately 50% bleach (125 g/L available chlorine), then in approximately 33% Hydrogen Peroxide with a final wash in 70% ethanol. This process was repeated with frequent inspections on a dissecting light microscope until as much debris and surface tissue could be removed as possible while endeavouring to minimise dislodgement or disturbance to the arrangement of the sclerites. If left to air-dry the sclerites tended to fall off, be pulled out of place or the polyps collapsed (Alderslade 1998) so twigs were first processed through a series of dehydration steps: 90% ethanol for 10 mins, 100% ethanol for 10 mins, two changes of dry 100% ethanol for 10 mins, 1:1 mixture of dry 100% ethanol and Hexamethyldisilazane (HMDS) for 10 mins, three changes of 100% HDMS for 10 mins and finally left to air dry. The twigs were then mounted vertically or obliquely on SEM stubs using a small amount of air drying silver conductive paint (from SPI Supplies) at room temperature which firmed sufficiently rapidly to hold each twig upright on immersion of the base of the twig. Once the glue was set, preparations were sputter-coated in gold and placed in the SEM. The orientation of the stubs could be adjusted to expose different views of the polyps and anthopomas. In some instances there was so little type material available that electron micrographs were not attempted.

3.2.5 Molecular Methods

Molecular data was obtained for a sub-set of specimens examined morphologically, in order to determine links between morphological and molecular groups within *Primnoisis*. Of the 171 specimens used for morphological taxonomic review, only samples which had been collected since 2000 were used for molecular analysis, because previous studies have shown that coral DNA degrades relatively quickly (Miller et al. 2010). Additionally, usually no records were kept of original preservation methods for older samples and there is potential that some may have been in formalin, thereby limiting the likelihood of successful DNA sequencing of relatively long gene regions (France & Kocher 1996).

3.2.5.1 Extraction, amplification, purification and sequencing

Total genomic DNA was extracted from a few polyps of each colony using the standard protocol of the Qiagen DNeasy Kit with the following adjustments: all samples were incubated overnight in the lysis buffer at 56°C, and during the final elution step, the AE buffer was warmed to approximately 50°C and the samples were left for 10 minutes before centrifuging, which significantly increased the final concentration of DNA (Helena Baird, pers. comm.). DNA quality was assessed visually on a 1% agarose gel and final concentration determined using a Nanodrop 8000 (ThermoScientific) and, if necessary, the DNA was diluted to a final concentration of 20–30ng/µl.

Two mitochondrial gene regions, igr1–COI and mtMutS (McFadden et al. 2011), were selected for the genetic analysis. The two regions combined are currently the most phylogenetically informative mitochondrial gene regions for octocorals and to date nuclear gene regions have proved difficult to reliably amplify and sequence (Baco & Cairns 2012; McFadden et al. 2011) although recent studies indicate 28S rDNA is potentially useful for phylogenetic analyses in octocorals (McFadden, Reynolds, et al. 2014; McFadden & van Ofwegen 2013). Attempts to amplify ITS, a nuclear region considered informative in many corals (McFadden et al. 2010; Miller, Rowden, Williams, & Häussermann 2011; Miller et al. 2010), during this study resulted in multi-copy sequences which were impossible to interpret reliably.

Initially, PCR reactions of 20µl contained 2µl of 10x polymerase buffer (Sigma-Aldrich Co. LLC.), 3.5-5.0 mM $MgCl_2$, 0.2µM of each primer (Table 3.1), 0.2-0.6µg bovine serum albumen, 250µM of each dNTP, 0.4µl of REDTaq DNA polymerase (Sigma Aldrich) and 0.4-2µl of DNA template (with the final amount of DNA template to be between 5 and 10ng). DNA templates were found to vary considerably in concentration and quality, and were particularly reflective of sample age and preservation. Thus quantity of DNA template used in the PCR reactions had to vary correspondingly and was adjusted across PCR reactions to optimise amplification success. The PCR conditions were as follows: 94°C for 5 min, then 34 cycles of a three-step program (94°C for 30 s, 48°C for 45s (mtMutS) or 54°C for 30s (igr1-CO1) and 72°C for 1 min), with a 10-min final extension at 72°C. Amplification success was confirmed by running PCR products on 1% agarose gels then viewing them under ultraviolet light. PCR products were purified using a QIAquick PCR purification kit (Qiagen) with the only modification to the kit instructions being the final elution in warm (~50°C) distilled water with the sample left for approximately 10 minutes before centrifugation. Samples were sequenced on an ABI3730xl 96-capillary sequencer at AGRF laboratories in Brisbane, Australia. Poor quality reads were excluded from the final analysis.

Samples which did not amplify with the above protocol were re-run using a modified PCR protocol containing 4µl of 5x polymerase buffer (Finnzymes Phire Reaction Buffer which contains 1.5mM $MgCl_2$ at final concentration), 0.5µM of each primer, 200µM of each dNTP, 0.4µl of Taq DNA polymerase (Finnzymes Phire Hot Start II) and 0.5-2µl of DNA template (with the final amount of DNA template to be between 5 and 10ng) in a total volume of 20µl. The PCR conditions were: 98°C for 30s, then 34 cycles of a three step program (98°C for 10s, 48°C (mtMutS) or 54°C (igr1-COI) for 10s and 72°C for 20-30s), with a 2 minute final extension at 72°C.

In some cases, the DNA proved too degraded to amplify across the entire length of the target gene region. Consequently, internal primers were designed based on entire sequences already obtained from less degraded samples. Primers were designed using the web-based software Primer3 v1.1.4 (http://frodo.wi.mit.edu/primer3/) and were situated in conserved regions approximately in the middle of the two mitochondrial gene regions (Table 3.1). These were used in conjunction with those primers from McFadden et al. (2011) such that two short halves of each gene region could be assembled into a complete longer sequence. The internal primers were only used with the second PCR protocol outlined above (Finnzymes Phire Hot Start II Taq).

Table 3.1. Primers used to amplify two mitochondrial gene regions (igr1–COI and mtMutS) including published external primers and newly designed internal primers. (adapted from McFadden et al. 2011)

Primer	**Sequence 5'→3'**	**No. of bps**	**T_m°**	**Reference**
COII(5')-igr1-COI(5'):				
1.1 kB				
1) COII8068F forward	CCATAACAGGACTAGCAGCATC	~1000 (1&4) ~ 570 (1&2)	62.5	McFadden et al. 2011
2) PRANCOIR reverse	CCTGTACCTGCCCCTTGTT		63.8	This study **(igr1–COIA)**
3) PRANCOIF forward	GGATTCGGAAATTGGTTTGT	~ 550 (3&4)	62.4	This study **(igr1–COIB)**
4) COIOCTR reverse	ATCATAGCATAGACCATACC			McFadden et al. 2011
mtMutS(5'):				
~760 nt				
5) ND42475F forward	TAGTTTTACTGGCCTCTAC	~990 (5&9) ~ 600 (5&7)	50.9	McFadden et al. 2011
6) ND42599F forward	GCCATTATGGTTAACTATTAC	~870 (5&9)	52.1	McFadden et al. 2011
7) PRIMMSH1R reverse	AGATACTGCGCGTTGTTTG			This study **(mtMutSA)**
8) PRIMMSH1F forward	GGTGACACCTCCCATTGAAC	~ 545 (8&9)	64.3	This study **(mtMutSB)**
9) MUT3458R reverse	TSGAGCAAAAGCCACTCC		61.6	McFadden et al. 2011

Sequences were assembled and edited using *MEGA* version 5 (Tamura et al. 2011). When available, contiguous sequences were constructed using forward and reverse primer sequences from the same PCR product. Where possible, short sequences generated by the internal primers were concatenated into a single long sequence for each gene region. After conducting BLAST searches in GenBank to confirm the validity of the sequences, the data were aligned in the software package MEGA5 using the alignment algorithm 'MUSCLE' (Edgar 2004) set with default parameters and then adjusted by eye if necessary and trimmed. The igr1 region contained a number of small INDELs which visibly corresponded with morphogroups. Though INDELS are often thought to be phylogenetically informative (Simmons, Ochoterena, & Carr 2001; Warnow 2012), many common models of phylogeny estimation treat them as missing data and exclude them from analysis. As yet there is no general consensus on the most biologically realistic and effective way to incorporate phylogenetic signal from INDELS (Saurabh, Holland, Gibb, & Penny 2012), but here INDELS were coded as binary events (each INDEL coded as present or absent) and converted into nominal nucleotides in the package FastGap 1.2 (Borchsenius 2009). This follows the 'simple indel coding' method in Simmons & Ochoterena (2000). After incorporation of the nominal nucleotides the sequences were analysed as detailed below.

A comparison of the number of variable nucleotide positions, parsimony informative sites and genetic distance from each gene region individually and with the two gene regions concatenated was conducted in MEGA5. For some specimens, only one gene region could be successfully sequenced. These specimens were excluded from the analysis of concatenated sequences. For some of the more degraded specimens, only half of a gene region was successfully sequenced so, rather than trimming all the sequences to the length of the very short sequences, all short sequences were extended to the length of the longer sequences with question marks denoting unknown nucleotides. Despite some evidence that, given enough characters in the overall analysis, including taxa with missing data does not decrease phylogenetic accuracy or support (Wiens & Morrill 2011), it was found that taxa missing the igr1 region particularly could not be reliably positioned and so were excluded. Genetic distance as uncorrected pairwise p-distances between groups was obtained from MEGA5 to allow comparisons with published sequence variability and genetic distances among and between octocoral species and genera. A character-based analysis (or a comparison of single nucleotide polymorphisms) between taxa was also employed as an additional species delineation tool. This approach has been considered useful when genetic distances and sequence variability are low (Baco & Cairns 2012; McFadden et al. 2011).

3.2.5.2 Outgroups and additional sequences

Sequences from GenBank of closely related species and genera were included in the phylogenetic analysis to help elucidate the relationships among the *Primnoisis* samples studied here (Table 3.2). In GenBank there were few relevant sequences of specimens considered to be from the family Mopseinae and no Mopseinae specimens had both mtMutS and igr1–COI gene regions sequenced. Thus four specimens from the closely related genus *Notisis* and a specimen morphologically determined to be from an undescribed Mopseinae genus (Alderslade pers. comm.) were sequenced using the first protocol at both gene regions and included as outgroups (Table 3.2). These specimens proved to have an entwined relationship with *Primnoisis* specimens, thus additional sequences from *Echinisis, Chathamisis* (mtMutS only) and *Keratoisis* were included in an attempt to elucidate intergeneric relationships.

Table 3.2. Details of additional sequences of related genera sourced from GenBank or generated within this study.

GenBank number	Gene Region	Species	Voucher specimen	Authors
KC660900	mtMutS	*Echinisis spicata*	NIWA 65216	Luisa Dueñas in press
KC660886	mtMutS	*Chathamisis bayeri*	NIWA 41543	Luisa Dueñas in press
KC660862	mtMutS	*Chathamisis* sp.	NIWA 15630	Luisa Dueñas in press
KC660882	mtMutS	*Notisis* sp.	NIWA 28364	Luisa Dueñas in press
	mtMutS	*Notisis* sp.	MNHN IK-2009-0285 (part)	This study
	igr1–COI	*Notisis* sp.	MNHN IK-2009-0285 (part)	This study
	mtMutS	*Notisis* sp.	MNHN IK-2009-0493	This study
	igr1–COI	*Notisis* sp.	MNHN IK-2009-0493	This study
	mtMutS	*New genus NIWA*	NIWA 39759	This study
	igr1–COI	*New genus NIWA*	NIWA 39759	This study
EF060025	mtMutS	*Keratoisis sp.MAN807-1*	YPM:IZ:35376	France, 2007
GU933628	igr1–COI	*Keratoisis D1a*	YPM:IZ:35376	McFadden et al. 2011

3.2.5.3 Phylogenetic Analyses

The most appropriate model for sequence evolution and phylogenetic reconstruction was assessed for each gene region using JModelTest v2.1.4 (Darriba et al. 2011; Guindon & Gascuel 2003) with default settings. The two gene regions were assessed separately for appropriate models as they may evolve differently. Based on Akaike Information Criterion (AIC) the most appropriate models were TPM1uf+G for the mtMutS gene region and TVM +I for igr1–COI. These models of evolution are not currently available in MrBayes so the next most optimal model suggested by JModeltest (GTR+G and GTR+I respectively) was employed. For the concatenated analysis, the sequences were partitioned and run using the recommended models for each partition.

Maximum likelihood (ML), conducted in MEGA5, and Bayesian analysis in the software package MrBayes v.3.1.2 (Huelsenbeck & Ronquist 2001), were used to construct phylogenetic trees for cladistic assessment of genus and species groupings. In MrBayes, priors were adjusted accordingly to implement the appropriate model. The Markov Chain Monte Carlo (MCMC) analysis was run with 2 runs, 4 chains, sample frequency of 100 and a burn-in of 25%. Analyses were run for the number of generations required to achieve an average standard deviation of split frequencies of 0.002

between the two runs. Phylogenetic trees were viewed and prepared for publication in FigTree v1.3.1 (Rambaut 2006-2009).

3.3 Results

3.3.1 Summary of taxonomic decisions

In total, 171 specimens were examined for this morphological taxonomic review. The genus *Primnoisis* has been retained, with many of the original species accepted as valid and only one synonymised (Table 3.3). However, it was not possible to confidently establish if *Primnoisis* is monophyletic as the molecular relationships with *Notisis* and an undescribed Mopseinae genus are unresolved. These three genera are closely related morphologically—all have anthopomas with octants consisting of a complex of longitudinally and obliquely arranged small sclerites, but *Notisis* specimens have spines on the internodes (considered a fundamental morphological difference with the Mopseinae) and two rows of sclerites in each tentacle, and the undescribed genus specimens have spiked sclerites which are absent in *Primnoisis.* The taxonomic definition of *Primnoisis* (see below) excludes these genera based on these morphological characteristics but the phylogenetic relationships remain uncertain. Of those specimens which were found to be within the morphological boundaries of *Primnoisis*, many divided clearly into two morphological and molecular groupings and two new subgenera, *Primnoisis* (*Primnoisis*) and *Primnoisis* (*Delicatisis*) are here established to reflect these groups.

The subgenus *Primnoisis* comprises two previously established species, *P. antarctica* and *P. fragilis,* and two new species, *P. chatham* and *P. erymna. P. sparsa* Wright & Studer, 1889 is synonymised with *P. antarctica.* These specimens are grouped on the morphological basis of usually robust, rigid colonies (Fig. 1A), large, mostly straight polyps (Fig. 1B), and sclerites in the form of large scales, in particular flattened, irregularly-shaped sclerites in the anthopoma (Fig. 1C, D). For those specimens where molecular results were obtained, sequences within this group differed by only a few nucleotides, if at all.

The new subgenus *Delicatisis* comprises the four established species, *P. rigida, P. delicatula, P. formosa* and *P. gracilis* (Gravier, 1913) (formerly *Mopsea gracilis*), and two new species, *P. niwa* and *P. millerae. Primnoisis* (*Delicatisis*) specimens have delicate, usually complex colonies (Fig. 1E) with small, tightly curved polyps (Fig. 1F) and small, usually warty polyp sclerites, particularly in the anthopoma where narrow, tuberculate rods are common (Fig. 1G, H). Molecular variation was slightly larger within the *P. (Delicatisis)* group than was found in the *P. (Primnoisis)* group. A key to species within *Primnoisis* was deemed ineffectual given the importance of qualitative sclerite form in distinguishing species and the heavy reliance on illustrations for differentiation.

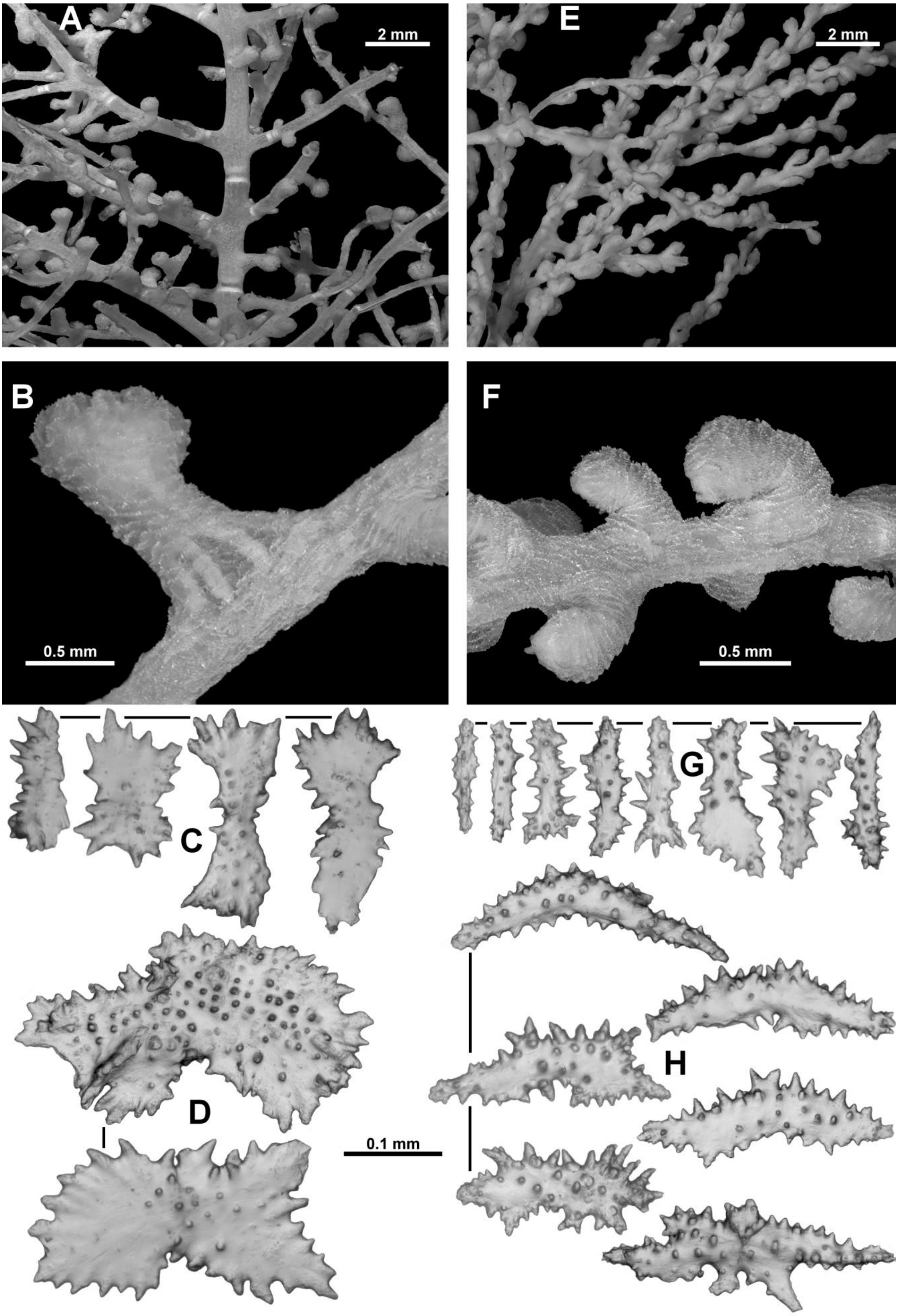


Figure 1. A–D. *P.* (*Primnoisis*) *antarctica* holotype: (A). Colony; (B). Polyp; (C). Anthopomal sclerites; (D). Polyp body sclerites. E–H. *P.* (*Delicatisis*) examples: (E). *P. gracilis* MNHN IK-2009-358 colony; (F). *P. formosa* holotype polyps; (G). *P. formosa* holotype anthopomal sclerites; (H). *P. formosa* holotype polyp body sclerites.

Primnoisis ambigua remains ungrouped at the subgenus level as it is represented by a single specimen (the holotype) across all collections inspected, and this specimen is anomalous for *Primnoisis*, having an almost planar colony form and a thick, opaque coenenchyme with extremely tuberculate sclerites. It strongly resembles *Notisis* specimens but lacks the spines on the internodes and has a single row of tentacle sclerites. The strong morphological resemblance between *P. ambigua* and *Notisis* specimens and the unresolved position of *Notisis* specimens in the phylogenetic analysis poses questions on the validity of *Notisis* relative to *Primnoisis* and the presumed phylogenetic importance of the spines on the axes.

Primnoisis mimas also is unplaced within the subgenera due to notable morphological differences from all other *Primnoisis* species such as large, fleshy polyps, a large number of transverse series of polyp body sclerites, 12–18 sclerites in the anthopoma (compared with 5–8 in the other species) and two rows of sclerites per tentacle. No specimens identified as *P. mimas* were available for the molecular analysis.

An additional new species, *Primnoisis tasmani*, is described but is unplaced at the subgenus level due to a lack of congruence between the morphological and molecular results. Morphologically this species fits neatly into the *P. (Delicatisis)* subgenus, but phylogenetically it is placed on a deep division, basal to all the other *Primnoisis* specimens (Figs. 3.75–3.77) and is inconsistently placed as more closely related to the undescribed Mopseinae genus.

Table 3.3. Summary of the taxonomic classification within *Primnoisis* of established species only.

Original designation	Author	Current or new designation
Primnoisis antarctica	Wright & Studer, 1889	*Primnoisis (Primnoisis) antarctica* Wright & Studer, 1889
Primnoisis sparsa	Wright & Studer, 1889	*Primnoisis (Primnoisis) antarctica* Wright & Studer, 1889
Primnoisis ambigua	Wright & Studer, 1889	*Primnoisis ambigua* Wright & Studer, 1889
Primnoisis rigida	Wright & Studer, 1889	*Primnoisis (Delicatisis) rigida* Wright & Studer, 1889
Primnoisis delicatula	Hickson, 1907	*Primnoisis (Delicatisis) delicatula* Hickson, 1907
Primnoisis fragilis	Kükenthal, 1912	*Primnoisis (Primnoisis) fragilis* Kükenthal, 1912
Mopsea gracilis	Gravier, 1913	*Primnoisis (Delicatisis) gracilis* (Gravier, 1913)
Primnoisis formosa	Gravier, 1913	*Primnoisis (Delicatisis) formosa* Gravier, 1913
Primnoisis mimas	Bayer & Stefani, 1987	*Primnoisis mimas* Bayer & Stefani, 1987

3.3.2 Systematic account

ISIDIDAE Lamouroux, 1812

Mopseinae Gray, 1870

***Primnoisis* Studer [& Wright], 1887**

Isis antarctica Studer, 1878: 661, Taf.V. Fig. 32.

Primnoisis Studer [& Wright], 1887: 46 [type species: *Isis antarctica* Studer, 1878 by designation]; Wright & Studer 1889: XLV, 33–35; Nutting 1910: 2–3; Kükenthal 1912: 339–340; Gravier 1914: 24–28; Kükenthal 1912: 339–340; 1915: 122; 1919: 611–612, 866; 1924: 432; Deichmann 1936: 250; Bayer 1955: 216; Grant 1976: 35; Bayer & Stefani 1987: 942–944; Alderslade 1998: 263.

Ceratoisis (part) Hickson 1907: 4–5.

Diagnosis: Delicate or robust, bottlebrush-shaped or bushy isidid colonies, often with a single main stem; branching on all sides of axis always from internodes, ramification usually up to 5 degrees; internodes with low longitudinal ridges but otherwise smooth; polyps arranged haphazardly throughout, clavate, standing perpendicular, oblique or acutely angled to axis; polyp body with overlapping, transverse, tuberculate scales, occasionally flattened spindles; continuous anthopomal octants consisting of a complex of narrow, tuberculate rods, irregular triangles, bent, flattened spindles and irregular scales often with a broad base, all arranged longitudinally to obliquely in anthopoma; tentacles with transverse, small, crescent-shaped scales usually arranged in a single row, but can be in two slightly overlapping rows per tentacle; coenenchyme consisting of interlocked, small, tuberculate scales and flattened rods, usually arranged longitudinally.

***Primnoisis* (*Primnoisis*) new subgenus**

Primnoisis (part) Studer [& Wright], 1887: 46; (part) Wright & Studer 1889: XLV, 33–35; (part) Nutting 1910: 2–3; (part) Kükenthal 1912: 339–340; (part) Gravier 1914: 24–28; (part) Kükenthal 1912: 339–340; 1915: 122; 1919: 611–612, 866; 1924: 432; (part) Grant 1976: 35; (part) Bayer & Stefani 1987: 942–944; (part) Alderslade 1998: 263.

Ceratoisis (part) Hickson 1907: 4–5.

Diagnosis:

As for the genus, except colonies usually robust, branches often rigid and stiff; clavate polyps large, often straight and stand perpendicular or obliquely to branch; some curved distally; polyp body sclerites tend to be large scales with minimal to extensive tuberculation; anthopomal sclerites are commonly large scales, often with a smooth, broadened base.

Etymology:

Contains the type species for *Primnoisis* thus is the nominotypical subgenus and is denoted by the same name as the genus.

Type species:

Primnoisis antarctica Wright & Studer, 1889 here designated.

***Primnoisis* (*Primnoisis*) *antarctica* Wright & Studer, 1889**

(Figs. 3.1–3.7)

Isis antarctica Studer, 1878: 661, Taf. V. Fig. 32.

Primnoisis antarctica Wright & Studer, 1889: 35–36, Pl. VIII Fig. 2, 2a, 2b, Pl. IX Fig. 6); ?Kükenthal 1912 [part]: 340–342, Taf. XXIII Figs. 18, 19, Figs. 55–57; ?Gravier 1913: 453; ?Gravier 1914: 28–31, Pl. III Fig. 12, Figs. 14–20; Kükenthal 1915: 123; 1919: 614; 1924: 434; Bayer 1955: 216, Pl. 6e; ?Eguchi 1964: 9, Pl. 1, Fig. 5; ?Grant 1976 [part]: 36–37, Figs. 31–32; ?Bayer & Stefani 1987: 944–946, Figs. 1a, 2, 3a, 3b, 4; Branch & Williams 1993: 15; Alderslade 1998: 263, Fig. 201.

Primnoisis sparsa Wright & Studer, 1889: 36–37, Pl. VIII Fig. 4, Pl. IX Fig. 7; Kükenthal 1915: 123; Kükenthal 1919: 614; Kükenthal 1924: 484; Thomson & Rennet 1931: 13; Branch & Williams 1993: 15; Alderslade 1998: 263.

NOT *Ceratoisis (Primnoisis) antarctica* Hickson 1907: 6-7, Pl. II Figs. 13–15.

NOT *Primnoisis antarctica* Thomson & Rennet 1931: 11.

Material examined:

Holotype: NHMUK 1889.5.27.24, colony portion, Prince Edward Island, southern Indian Ocean, HMS *Challenger*, stn. 145A, 46.683°S, 38.167°E, depth 567 m, 27th Dec 1873; **NHMUK 1986.12.16.16**, slide of twigs from *P. antarctica* holotype; **NHMUK 1889.5.27.27b**, slide of twigs of *P. antarctica* and *P. sparsa* holotypes and *P. rigida* syntype.

Other material: *P. sparsa* NHMUK 1889.5.27.26, colony portion and slide of holotype, off Prince Edward Island, HMS *Challenger*, stn. 145A, 46.683°S, 38.167°E, depth 155? m, 27th Dec 1873?.

Material found to be incorrectly determined:

ZMB 5453, Gauss Station, Antarctica, Deutche Sudpolar-Expedition 1901–1903, 385 m, 24th Jan 1903 (Kükenthal 1912) => *P. formosa.*

NHMUK 1907.06.12.11, determined as *P. antarctica* in Hickson 1907, McMurdo Bay, Antarctica, *Discovery* Expedition, RRS *Discovery,* 77.63°S, 165.42°E, depth 176–219 m, 8th Feb 1902 => *P. fragilis.*

AM G.13226, determined as *P. antarctica* in Thomson & Rennet (1931), Commonwealth Bay, Adelie Land, Antarctica, Australian Antarctic Expedition, stn. 8, 66.1°S, 94.3°E, depth 219 m, 27th Jan 1914 => *P. fragilis.*

AM G.13230, **G.13244** & **G.13278**, determined as *P. sparsa* by Thomson & Rennet (1931), Commonwealth Bay, Adelie Land, Antarctica, Australian Antarctic Expedition, stn. 1–D, 66.833°S, 142.1°E, depth 640 m, 22nd Dec 1913 => *P. fragilis.*

AM G.13280, determined as *P. sparsa* in Thomson & Rennet (1931), Commonwealth Bay, Adelie Land, Antarctica, Australian Antarctic Expedition, stn. 1–D, 66.833°S, 142.1°E, depth 640 m, 22nd Dec 1913 => *P. gracilis.*

NIWA 28309, determined as *P. antarctica* in Grant (1976), Moubray Bay, Ross Sea, Antarctica, stn. E188, 72.179°S, 170.807°E, depth 353 m, 20th Jan 1965 => *P. fragilis.*

?AM G.13229, determined as *P. sparsa* in Thomson & Rennet (1931), Commonwealth Bay, Adelie Land, Antarctica, Australian Antarctic Expedition, stn. 3, 66.5°S, 141.7°E, depth 287 m, 31st Dec 1913 (many fragments and dislodged polyps, possibly from two different species, neither of which are likely to be *P. antarctica* but it was not possible to identify them with any certainty).

Description:

Colony form:

The holotype consists of three colony portions, each with a general bottle-brush form, although one piece appears to be tangled with loose fragments (Fig. 3.1A, B). The colony portion examined here is approximately 60 mm long and 30 mm at the widest point, tapering distally (Fig. 3.1C). It is in reasonable condition with many polyps remaining and a significant amount of coenenchyme still intact. There is a robust main branch, broken at the base, which has a diameter of 1.1 mm proximally, tapering to 0.6 mm distally. Most commonly, 4–5 primary branches emanate from each internode of the main branch, although there can be between 2–8 branches per internode. Branches arise at approximately 60–90° on all sides and throughout each internode (Fig. 3.1D). This differs from the original description where Wright and Studer, (1889) specify branch angles of 35–40° and suggest there is a tendency for opposite branches to be “stronger than the others”. Primary branches extend up to 25 mm from the main branch although many are broken. From some of the primary branches, secondary branches (up to 2 per internode) occur. Most of the secondary branches are broken distally and only a single example of tertiary branching was found. Secondary branches are up to 14 mm long, unbranched and taper to a narrow point. Wright & Studer (1889) state that ramification up to the fourth order was observed in the holotype in its original condition. Polyps are cream to light beige, denuded internodes are off-white, nodes are dark brown in the centre grading to golden brown with a narrow strip of iridescence at the junction with the internodes.

Polyps:

Polyps are sparse, particularly on the main branch which has 0–2 polyps per internode and up to 2–3 polyps per internode on the distal branches. There is 2–3 mm between polyps and they are distributed on all sides of the branches, not in spirals as suggested by Wright & Studer (Fig. 3.1D). The polyps are tall, straight and clavate with a slightly constricted neck below the rounded polyp head and a broadened base (Fig. 3.2A–C). They mostly stand close to perpendicular to the axes although some are obliquely placed particularly on the distal twigs. At the twig tip, a terminal polyp occurs a short distance from the actual tip, the twig then tapering to a point (Fig. 3.2B). All polyps are almost translucent under a dissecting microscope. Adult polyps range from 0.8–1.5 mm long, 0.5–0.8 mm diameter at the head and 0.35–0.6 mm diameter at the neck. There are numerous juvenile polyps, approximately 0.25–0.5 mm tall and 0.2–0.4 mm wide, scattered amongst the larger polyps. Almost all of the polyps have the tentacles folded inwards across the mouth covered by the anthopomal sclerites.

Axis:

Proximally in the colony, the internodes are essentially circular in cross-section, and almost square in cross-section at the distal twigs (Fig. 3.2D, E). The widest internode (1.1 mm in diameter), at the base of the specimen, has about 20 low primary ridges, the number of which decreases with width of the internode to 12 ridges for a 0.4 mm diameter internode, otherwise the internodes are without ornamentation. On the central branch internodes are 2.8–5.5 mm long and nodes are 0.2–0.45 mm long. On the primary branches internodes are mostly 3–3.5 mm long and nodes 0.15–0.25 mm long. The diameter of the primary branches available here is approximately 0.5 mm proximally tapering to 0.2 mm distally. The branches are robust and quite stiff.

Sclerites:

The polyps are covered in a single layer of translucent sclerites. On the polyp body, sclerites are arranged in more or less transverse series, slightly overlapping the sclerites above (Fig. 3.2A–C) but are longitudinal to oblique in the anthopoma (Fig. 3.2F, G). Adult polyps have between 10–20 irregular series of sclerites, juvenile polyps have fewer.

The complex anthopoma is symmetrical and relatively consistently arranged with no obvious difference between abaxial and adaxial sides (Fig. 3.2F). Each octant consists of 6–8 small sclerites arranged obliquely at the base of the octant and longitudinally at the tip (Fig. 3.2G). Sclerites consist of a mixture of irregular rectangles and triangles (Fig. 3.3). Some have well developed spines around one end, like a splayed hand, and these interlock with adjacent sclerites. Sclerites are 0.12–0.26 mm long with the larger ones more common proximally in the anthopoma. Some of the anthopomal sclerites are relatively warty, especially compared with the polyp body sclerites. The anthopoma is continuous with the polyp body sclerites with smaller, crescentic to irregularly triangular sclerites (Fig. 3.3Aa) occurring at the transition between the longitudinal anthopomal sclerites and the transverse body sclerites.

Small, thin, crescent-shaped sclerites with no or minimal tubercles are arranged transversely in a single row along each tentacle (Fig. 3.3B). They are approximately 0.03–0.06 mm high and 0.07–0.125 mm long and many have pronounced but short spines in the upper edge.

There are no sclerites in the mesenteries contrary to the statement of Wright & Studer (1889).

Body sclerites are chiefly relatively large, somewhat rectangular or oval scales with only a few minor tubercles and rounded spines of various lengths along their border (Fig. 3.4). They are thin and easily broken. There are also narrower, more tuberculate sclerites which occur more commonly around the base of the polyps (Fig. 3.4a). Wright & Studer (1889) mentioned many lobed sclerites, described as having an “upper toothed edge which is almost straight or slightly indented, and a lower edge, which is divided into two lobes by a more or less deep incision” (Fig. 3.4b). Some sclerites have large, pronounced spikes on the margins often, but not consistently, more pronounced on the distal edge. Apart from this, unlike the polyp body scales in, for example, species of *Pteronisis,* there is generally little difference between the proximal and the free distal edges of the sclerites, making it difficult to be confident on original orientation. The largest, flat sclerites are approximately 0.11–0.24 mm high and 0.23–0.34 mm long with an average height to length ratio of 0.54.

Coenenchymal sclerites are mostly narrow, flattened, tuberculate rodlets (Fig. 3.5) although there are some slightly larger, irregular rectangles and a few forked sclerites. They are approximately 0.14–0.3 mm long, and are moderately tuberculate with some minor marginal spines.

Intracolonial variation appears relatively minor but there are some polyps with slightly more tuberculate sclerites particularly in the anthopoma (Fig. 3.6). Thick, tuberculate rods, some with broadened ends, can occur in the anthopoma (Fig. 3.6Aa) and the polyp body sclerites can be more rugged with robust, rounded marginal spines and a slightly more extensive coverage of tubercules (Fig. 3.6B).

Variability:

An examination of the holotype of *Primnoisis sparsa* Wright & Studer, 1889 showed that the species should be synonymised with *P. antarctica*. The holotype lot includes a large Primnoidae colony as well as a small *Primnoisis* colony portion (Fig. 3.7A). The portion is lacking a holdfast and is a bottlebrush shape with many broken branches, however there is evidence of up to 12 branches per internode on the main branch. There are very few polyps remaining on the colony but there are numerous dislodged polyps. Polyps are almost perpendicular to the branches, straight and relatively tall, up to 1.7 mm (Fig. 3.7B). The colony portion appears to have been poorly preserved or preserved in a medium different to *P. antarctica* despite being collected on the same voyage at a nearby site, and the sclerites are yellowy-brown and opaque under transmitted light. The anthopomal sclerites are similar to those of the *P. antarctica* holotype—mostly scales with large, marginal spines, some small triangles with spines on a single margin and a few narrow rods (Fig. 3.7C). Tentacles sclerites also resemble those of the *P. antarctica* holotype (Fig. 3.7D). The polyp body sclerites are large scales like those of the *P. antarctica* holotype but tend to have a more substantial covering of tubercles and large, more robust marginal spines. Wright & Studer differentiated it from *P. antarctica* by the "sparser manner of branching, the form of the polyps, and the nature of the scales of the calyx, which here appear to be rough and spiny". These reasons lack veracity as the colony has evidence of similar number of branches per internode to that of *P. antarctica*, the polyps of the two colonies are similar in shape and although the sclerites of the *P. sparsa* holotype are more "rough and spiny" there is intracolonial variation within the *P. antarctica* holotype which reflects similarly more robust and spiny sclerites.

Distribution:

Subantarctic waters around the Prince Edward Islands and Heard and Macdonald Islands.

Depth:

155–567 metres.

Remarks:

Historically, specimens have been determined as *P. antarctica* from all around the Antarctic continent and from some subantarctic islands. The colony and polyp form (rigid, bushy isidid colonies with large, straight, slightly clavate polyps) is common throughout these areas but sclerite form across these colonies displays a large range of shapes, size, spininess and coverage of tubercles. *P. antarctica sensu strict*o has large, flat body sclerites, with rounded, large marginal spines and irregularly rectangular scales in the anthopoma and that definition excludes many of those colonies historically determined as *P. antarctica.* It is entirely possible that this species is restricted to Prince Edward Island and nearby subantarctic islands and is not common. However, variability of sclerites including intracolonial variation means it is possible that specimens with similar colony form but with much more tuberculate sclerites may also be this species (see *P.* cf. *antarctica* below).

Many specimens previously determined as *P. antarctica* are here included as *P. fragilis.* This species also has large body and anthopoma sclerites but these are usually more tuberculate and more irregular than those from *P. antarctica. P. fragilis* colonies are more delicate and flexible, with fewer branches per internode and more crowded, strongly clavate polyps, especially at the branch tips. Additionally the polyps in *P. fragilis* tend to angle distally, although this can vary throughout a colony with perpendicular polyps occurring proximally. Another similar species to *P. antarctica* is *P. chatham* n. sp.*,* distinguished by its distribution (Chatham Rise, New Zealand), smaller body sclerites with somewhat serrated edges instead of large, rounded marginal spines, and its large, robust, rounded anthopomal sclerites. *P. erymna* n. sp. is distinguished from *P. antarctica* by its large, robust, rounded sclerites in the anthopoma and on the polyp body. Other *Primnoisis* species belong to the other subgenus, *Delicatisis,* and have smaller, acutely curled polyps and much smaller sclerites, usually with more crowded warts and spines.

Kükenthal (1912) mentioned that several examples of *P. antarctica* were collected during the Deutschen Subpolar-expedition. His figure of *P. antarctica* (p.341, fig. 53) depicts the sclerites as arranged transversely on the back of the tentacles, suggesting something other than *Primnoisis.* One of these specimens (ZMB 5453) was examined and was found to be a specimen of *P. formosa* and has an anthopoma consisting of longitudinal to obliquely arranged sclerites. Thus the depiction of the anthopoma in Kükenthal (1912) must be considered inaccurate*.* Similarly, Hickson (1907) depicted a specimen identified as *P. antarctica* (Pl. II, Fig. 15) and stated that for *P antarctica* specimens “scales on the back of the tentacles are all horizontally placed” (although this may have been a reference to the transverse scales in the tentacles). On examination of one of these specimens, it was found to be a specimen of *P. fragilis* with longitudinally to obliquely placed anthopoma sclerites, thus Hickson’s figure and description of the sclerites on the back of the tentacle must also be considered inaccurate.

Primnoisis cf. *antarctica*

(Figs. 3.8–3.10)

Material examined:

SAM H.17941, ~55 nautical miles NW of Heard Island, southern Indian Ocean, RV *Aurora Australis*, stn. 61, 52.567°S, 72.3°E, depth 655–800 m, 11th June 1999; **NTM CO12329**, NW of Heard Island, southern Indian Ocean, RV *Aurora Australis*, stn. 61, 52.567°S, 72.3°E, depth 655–800 m, 11th June 1999; AAD unregistered, Aurora Bank, Heard Island, Southern Ocean, FV *Southern Champion,* voyage 26, stn. 179, (**SC26 179**), 52.482–52.487°S, 71.750–71.756°E, depth 272–275 m, 1st May 2003; AAD unregistered, Aurora Bank, Heard Island, Southern Ocean, FV *Southern Champion,* voyage 26, stn. 194, (**SC26 194**), 52.467–52.487°S, 71.733–71.7588°E, depth 268–275 m, 2nd May 2003; AAD unregistered, Coral Bank, Heard Island, Southern Ocean, FV *Southern Champion,* voyage 26, stn. 214, (**SC26 214**), 51.869–51.863°S, 71.285–71.292°E, depth 282–298 m, 3rd May 2003; AAD unregistered, Coral Bank, Heard Island, Southern Ocean, FV *Southern Champion,* voyage 26, stn. 216, (**SC26 216**), 51.938–51.944°S, 71.286–71.287°E, depth 292 m, 4th May 2003; AAD unregistered, Coral Bank, Heard Island, Southern Ocean, FV *Southern Champion,* voyage 26, stn. 219, (**SC26 219**), 52.053–52.057°S, 71.448–71.454°E, depth 291–288 m, 4th May 2003; AAD unregistered, Southern Shell Bank, Heard Island, Southern Ocean, FV *Southern Champion,* voyage 26, stn. 253, (**SC26 253**), 51.911–51.908°S, 77.112–77.121°E, depth 341–332 m, 8th May 2003; AAD unregistered, Southern Shell Bank, Heard Island, Southern Ocean, FV *Southern Champion,* voyage 26, stn. 255, (**SC26 255**), 51.828–51.827°S, 76.908–76.901°E, depth 290–286 m, 8th May 2003; AAD unregistered, Southern Shell Bank, Heard Island, Southern Ocean, FV *Southern Champion,* voyage 26, stn. 267, (**SC26 267**), 51.817–51.82°S, 76.019–76.027°E, depth 472–447 m, 10th May 2003; AAD unregistered, Southern Shell Bank, Heard Island, Southern Ocean, FV *Southern Champion,* voyage 26, stn. 268, (**SC26 268**), 51.753–51.748°S, 76–75.997°E, depth 433–363 m, 10th May 2003; AAD unregistered, Southern Shell Bank, Heard Island, Southern Ocean, FV *Southern Champion,* voyage 46, stn. 112, (**SC46 112**), 51.815–51.825°S, 76.210–76.199°E, depth 283 m, 24th June 2007; AAD unregistered, Evitas, Heard Island, Southern Ocean, FV *Southern Champion,* voyage 50, stn. 43, (**SC50 43**), 52.77–52.773°S, 74.652–74.663°E, depth 285–288 m, 3rd June 2008; **?AM G.13236 (part)**, off Maria Island, Tasmania, Australia, Australian Antarctic Expedition, 42.6°S, 148.1°E, depth 118–2377 m, 13th Dec 1912 => many fragments and dislodged polyps, probably from two different species (*P. tasmani* n. sp.).

These specimens are grouped as a variation of *P. antarctica*, as they resemble it in colony form and polyp shape and size but vary slightly from it in the form of the anthopomal and polyp body sclerites. This variety is common in waters around Heard and Macdonald Island and off the east coast of

Tasmania (although that sample is in very poor condition). The group have robust colonies, rigid branches and reasonably sparsely distributed, clavate polyps which usually angle distally (Fig. 3.8A–C). However, many colonies demonstrated distinct variability in sclerite form within a single colony and establishing the general sclerite form to be confident of a distinct species proved difficult. It is possible these colonies are simply examples of *P. antarctica* (note Fig. 3.8D–G cf. Fig. 3.6A–C) but the anthopomal sclerites are usually large, tuberculate, rounded, robust rods and triangles (Figs. 3.8D; 3.9A) while anthopomal sclerites in *P. antarctica* are more commonly flattened scales (Fig. 3.3A). Additionally, in this variety the polyp body sclerites tend to have smaller marginal spines than in *P. antarctica*, similar to polyp body sclerites from *P. chatham* n. sp. (Fig. 3.21). One specimen has sclerites which are very similar to those from the *P. antarctica* holotype with large, rounded marginal spines on wide scales from the polyp body and wide, irregularly rectangular scales with largely smooth, broadened ends from the anthopoma (Fig. 3.10B–D) but this specimen consists only of small, damaged twigs with few remaining polyps (Fig. 3.10A).

These specimens are kept separate here in the hope that future work with fresh specimens, particularly from the Prince Edward or Heard Island area, may be able to combine molecular and morphological results to elucidate species boundaries, in particular between *P. antarctica* and *P. chatham* n. sp.

***Primnoisis* (*Primnoisis*) *fragilis* Kükenthal, 1912**
(Figs. 3.11–3.18)

Primnoisis fragilis Kükenthal 1912 [part]: Taf. XXIII Fig. 20, textfigs. 58–60; 1915: 123; 1919: 616; 1924: 431; Thomson & Rennet 1931 [part]: 12; Alderslade 1998: 263.

Material examined:

Lectotype: ZMB 5461, Gaußstation, Antarctica, Deutche sudpolar expedition 1901-1903, approximately 66.03°S, 89.63°E, 350–385 m, 12th Jan 1903.

Other material: NHMUK 1907.06.12.11, determined as *P. antarctica* by Hickson (1907), McMurdo Bay, Antarctica, *Discovery* Expedition, RRS *Discovery,* 77.63°S, 165.42°E, depth 176–219 m, 8th Feb 1902; **AM G.13226**, determined as *P. antarctica* by Thomson & Rennet (1931), Commonwealth Bay, Adelie Land, Antarctica, Australian Antarctic Expedition, stn. 8, 66.1°S, 94.3°S, depth 219 m, 27th Jan 1914; **AM G.13230**, **G.13244** & **G.13278**, determined as *P. sparsa* by Thomson & Rennet (1931), Commonwealth Bay, Adelie Land, Antarctica, Australian Antarctic Expedition, stn. 1–D, 66.833°S, 142.1°E, depth 640 m, 22nd Dec 1913; **SAM H.17956**, Shackleton Iceshelf, BANZARE, stn. 100, 65.8°S, 89.717°E, depth 393 m, 3rd Nov 1931; **MV F76939**, Prydz Bay, Antarctica, RV *Aurora*

Australis, AA93, stn. 11A, 68.573°S, 77.638°E, depth 390 m, 17th Jan 1993; **MV F173634 (part)**, central Prydz Channel, Prydz Bay, Antarctica, RV *Aurora Australia,* ANARE AA97, stn. 11, 67.188–67.190°S, 70.294–70.304°E, depth 544 m, 22nd Feb 1997; **TMAG K4286**, Commonwealth Bay, Terra Adelie, Antarctica, CEAMARC, stn. 039–141, 66.55–66.58°S, 143.959–143.087°E, depth 866 m, 27th Dec 2007; **TMAG K4287** & **MNHN IK-2009-0314**, Commonwealth Bay, Terra Adelie, Antarctica, CEAMARC, stn. 048–194, 66.939°S, 144.686–144.621°E, depth 409–326 m, 28th Dec 2007; **TMAG K4288**, Commonwealth Bay, Terra Adelie, Antarctica, CEAMARC, stn. 002–416, 66.001–66.0°S, 141.354–141.299°E, depth 229–232 m, 12th Jan 2008; **TMAG K4289** & **MNHN IK-2009-0434**, Commonwealth Bay, Terra Adelie, Antarctica, CEAMARC, stn. 072–456, 66.341–66.34°S, 140.446–140.524°E, depth 330–444 m, 14th Jan 2008; **MNHN IK-2009-0326**, Commonwealth Bay, Terra Adelie, Antarctica, CEAMARC, stn. 012-431, 66.55°S, 140.85°E, depth 151–361 m, 13th Jan 2008; **MNHN IK-2009-0292**, Commonwealth Bay, Terra Adelie, Antarctica, CEAMARC, stn. 010–420, 66.33°S, 141.333°E, depth 207–227 m, 13th Jan 2008; **MNHN IK-2009-0342**, Commonwealth Bay, Terra Adelie, Antarctica, CEAMARC, stn. unknown, Jan 2008; **TMAG K4291**, Tressler Bank, Shackleton Iceshelf, Antarctica, RV *Aurora Australis,* V2 East Antarctica, stn. BTC07, 64.284–64.283°S, 97.120–97.109°E, depth 637–709 m, 2nd Jan 2010; **TMAG K4292**, Tressler Bank, Shackleton Iceshelf, Antarctica, RV *Aurora Australis,* V2 East Antarctica, stn. BTC18, 64.563–64.566°S, 95.321–95.31°E, depth 710–729 m, 3rd Jan 2010; **TMAG K4293**, Tressler Bank, Shackleton Iceshelf, Antarctica, RV *Aurora Australis,* V2 East Antarctica, stn. BTC20, 64.803–64.801°S, 94.177–94.192°E, depth 447–443 m, 4th Jan 2010; **TMAG K4294**, Tressler Bank, Shackleton Iceshelf, Antarctica, RV *Aurora Australis,* V2 East Antarctica, stn. BTC22, 64.789–64.791°S, 94.156–94.140°E, depth 690–693 m, 4th Jan 2010; **TMAG K4295 & K4305**, Shelf break canyon, Wilhelm II Land, Antarctica, RV *Aurora Australis,* V2 East Antarctica, stn. BTC30, 65.836–65.834°S, 89.541–89.544°E, depth 547–502 m, 8th Jan 2010; **NIWA 28309**, Moubray Bay, Ross Sea, Antarctica, stn. E188, 72.179°S, 170.807°E, depth 353 m, 20th Jan 1965; **NIWA 28401** & **NIWA 28402**, Sabrina Island, Balleny Islands, Antarctica, RV *Tangaroa,* stn. 442, (TAN0602/442), 66.756°S, 163.06°E, depth 140–150 m, 10th Mar 2006; **NIWA 36876** & **NIWA 41864**, Ross Sea, Antarctica, RV *Tangaroa,* stn. 100, (TAN0802/100), 76.202°S, 176.248°E, depth 451–447 m, 18th Feb 2008; **NIWA 37677**, Ross Sea, Antarctica, RV *Tangaroa,* stn. 161, (TAN0802/161), 72.076°S, 172.904°E, depth 535–536 m, 24th Feb 2008; **NIWA 65175**, Ross Sea, Antarctica, TRIP 2732, stn. 57, 72°S, 176°W, 18th Jan 2009; **SIO Co2492**, South Sandwich Ridge, Scotia Arc, RVIB *Nathaniel B Palmer*, stn. SS2a-36, 58.3773°S, 26.2824°W, depth 153–420 m, team led by Dr Nerida Wilson & Dr Greg Rouse, 5th Oct 2011; **SIO Co2483**, South Sandwich Ridge, Scotia Arc, RVIB *Nathaniel B Palmer*, stn. SS2a-37, 58.3758°S, 26.2837°W, depth 152–156 m, team led by Dr Nerida Wilson & Dr Greg Rouse, 6th Oct 2011; **SIO Co2468**, South Sandwich Ridge, Scotia Arc, RVIB *Nathaniel B Palmer*, stn. SS2a-38, 58.3785°S, 26.2834°W, depth 134–260 m, team led by Dr Nerida Wilson & Dr Greg Rouse, 6th Oct

2011; **SIO Co2479**, South Sandwich Ridge, Scotia Arc, RVIB *Nathaniel B Palmer*, stn. SS2a-39, 58.3680°S, 26.2813°W, depth 256–141 m, team led by Dr Nerida Wilson & Dr Greg Rouse, 6th Oct 2011; **SIO Co2521**, South Sandwich Ridge, Scotia Arc, RVIB *Nathaniel B Palmer*, stn. SS3-49, 59.3995°S, 27.2789°W, depth 143–169 m, team led by Dr Nerida Wilson & Dr Greg Rouse, 8th Oct 2011.

Material found to be incorrectly determined:

Syntype ZMB 5460, Gaußstation, Antarctica, Deutche sudpolar expedition 1901-1903, approximately 66.03°S, 89.63°E, depth 350-385 m, 12th Jan 1903 => *Primnoisis formosa.*

AM G.13204, Commonwealth Bay, Adelie Land, Antarctica, Australian Antarctic Expedition, stn. 1–D, 66.833°S, 142.1°E, depth 640 m, 22nd Dec 1913 => *P. formosa* and *P. gracilis.*

Description:

Kükenthal (1912) mentioned he had two specimens at his disposal for the description but then based his description on one of these without specifying which one. These two syntypes (ZMB 5461 and ZMB 5460) are here found to be different species. Kükenthal's colony figure (Taf. XXIII Fig. 20) matches that of the colony ZMB 5461 so this description is based on that specimen which is here designated as the lectotype. The other syntype, ZMB 5460 is a specimen of *P. formosa* and is removed from *P. fragilis.*

Colony form:

The colony is a bottle-brush form with a central main stem with relatively short side branches emanating on all sides (Fig. 3.11A, B). The whole colony is curved from jar storage and conforms to the original description. It is approximately 150 mm long (10 cm according to Kükenthal) with the base missing and it is approximately 60 mm across at the widest point. The primary branches all originate from the internodes at an angle between 45–60° and extend a relatively consistent length of approximately 30 mm (Fig. 3.11B). Secondary branching is very rare. There are many primary branches on the main stem, between 4 and 13 per internode, making the colony quite bushy and crowded. At the base of the central axis is a single example of anastomoses between two lateral branches. The specimen is in good condition with many branches and polyps remaining and much of the coenenchyme intact.

Internodes are white to grey, nodes are light golden-brown and polyps and coenenchyme are white to light cream.

Polyps:

On the central axis of the colony polyps are very rare with often no, or occasionally one, polyp per internode, but on the lateral branches there are often up to 15 polyps per internode, especially on the distal branches making the polyps at the top of the colony much more crowded than those at the base (Fig. 3.11A). Some polyps are angled at 45–90° to the branches but most polyps are curved distad at approximate angles of 30–45° to the branches (Fig. 3.11C–F). They are particularly abundant towards the tapering tips of the twigs (Fig. 3.11E, F). The polyps are often strongly clavate, with an obvious neck and the heads of the curved polyps do not usually touch the branches (Fig. 3.11G). Kükenthal depicted a single polyp somewhat similar to this—distinctly clavate (almost funnel-shaped), with the polyp bent almost at right-angles to the axis. This is the dominant shape of the polyps, particularly distally in the colony; however proximally, there are numerous polyps which are straighter and less clavate, standing almost perpendicular from the branches (Fig. 3.12A). There is up to 1.5 mm space between polyps. According to Kükenthal (1912), polyps are approximately 1.2 mm long which corresponds with measurement taken here (0.58–1.1 mm). The relatively broad polyp heads have diameters of 0.46–0.67 mm. Occurring throughout are many brooding polyps which are cylindrical with a modified rounded head and lack a neck (Fig. 3.11Fa). In the rest of the polyps, the tentacles fold over the polyp mouth to form a slightly rounded to almost flat polyp summit.

Axis:

The internodes of the main stem have low primary ridges and are basically circular in cross-section, while the distal internodes grade from circular to square in cross-section with only four primary corner ridges. Other than the ridges, the internodes are without ornamentation. All branching is from the internodes with a short calcareous piece beginning each branch. On the main stem most of the internodes are 8–12 mm long (although slightly shorter internodes were found) and are 1–1.5 mm in diameter. On the branches the internodes are slightly longer than those in the central axis but with a similar diameter.

Sclerites:

Polyps and colony surface are covered in a thin layer of sclerites. Polyps have slightly overlapping transverse scales, arranged in 11–13 irregular series between the polyp base and the anthopoma. There is little or no difference between the abaxial and adaxial sides of the polyp.

The anthopoma is complex with 5–7 sclerites effectively locked together to form each octant. They tend to be arranged obliquely at the proximal end of the octant and longitudinally at the distal end (Fig. 3.12B) and are large scales and rods with pronounced marginal spines which are often longer or more obvious at the ends of the sclerites (Fig. 3.12C). These sclerites are mostly 0.13–0.25 mm long. There are also irregularly crescentic sclerites, also with pronounced marginal spines, which occur at the junction between the obliquely arranged anthopomal sclerites and the transverse body sclerites (Fig. 3.12Ca).

The tentacles have a row of transverse crescentic scales with regular spines or protrusions around the edges, particularly on the distal edge, and minimal tubercles on the sclerite surface (Fig. 3.12D). These sclerites are 0.07–0.14 mm long.

The polyp body has large, jagged-looking scales with significantly more developed marginal spines—some have sharp spines and deep indentations while others have smooth, rounded spines (Fig. 3.13). The spines are usually larger on the distal edge of the sclerites and some sclerites have a narrow waist. The spines are quite visible on the polyps, being particularly noticeable on sclerites close to the anthopoma (Fig. 3.12A, B). The widest sclerites are generally found distally on the polyp, with sclerite width decreasing further down the polyp so that close to the base of the polyp the sclerites are narrow with fewer pronounced spines and smaller, regular tubercles (Fig. 3.13a). Sclerites are 0.21–0.4 mm long and 0.08–0.15 mm high at their widest point with a height to length ratio of 0.353. Considerable within-colony variability was evident in another polyp which had sclerites with significantly more tubercles on the sclerites (Fig. 3.14A–C).

The coenenchyme has short, flat rods and scales with simple, small tubercles, arranged in a single layer over the colony surface (Fig. 3.14D). The scales tend to be irregular shapes with jagged edges while some sclerites are simple rods with straight edges. There does not appear to be any pattern or predictable arrangement of the different sclerites within the coenenchyme. Lengths vary from 0.09–0.28 mm.

Variability:

There was considerable variation observed in the polyp body sclerites amongst the material examined and the group may represent a species complex. Variation was not consistent enough to separate the samples into predictable groupings, and genetically many samples had identical (or very close to identical) sequences across both gene regions and across great geographic distances. Growth form varies slightly as in the flexibility of the colonies and branching complexity but all have a bottle-brush form with wide-angled primary branching (Fig. 3.15A–C). The colonies are usually robust and reasonably stiff, but some have numerous, fragile or brittle distal branches while in others these are more flexible.

Proximally on the colonies, polyps are often only slightly clavate and straight, emanating at close to 90° from the branches (Fig. 3.15D). Closer to the branch tips the polyps are more acutely angled with a narrower neck and are more strongly clavate like those in the lectotype (Fig. 3.15E–G).

Some colonies included had sclerites very similar to those of the lectotype with sharp marginal spines and well-developed tubercles on the large scales from the anthopoma and polyp body (Fig. 3.16A–C) while other specimens had sclerites which were smoother with fewer tubercles and less complex marginal spines (Fig. 3.16D–F). Sclerite variation did not correspond with geographic distribution or colony differences and all the colonies pictured here (Figs. 3.15–3.18) have identical or close to identical gene sequences (see section 3.3.3).

A few colonies have noticeably tall polyps with very narrow body sclerites that have an almost smooth surface and much smaller tubercles than those in the lectotype. One example, MNHN IK-2009-342, has a colony form which is similar to the lectotype (Fig. 3.15C) but the polyps tend to be taller and more crowded than in the lectotype (Fig. 3.17A, B), with approximately 20 irregular series of narrow body sclerites (Fig. 3.17C). Some are more strongly clavate like those common in the lectotype (Fig. 3.17D). The anthopomal and tentacular sclerites are similar to those of the lectotype (Fig. 3.17E, F) but the distal body sclerites have fewer surface tubercles, while the proximal body sclerites are long, narrow, tuberculated rods and have somewhat serrated margins and only minor marginal spines (Fig. 3.17G).

Specimens from the Scotia Arc on the Antarctic Peninsula had identical (or close to) sequences to those specimens from Eastern Antarctica. Unfortunately, the whole colonies were not available for examination, but the small twig fragments examined have numerous polyps that show a similar shape to those of the lectotype (Fig. 3.18A, B) although the polyps are not as crowded and are not as strongly curved when compared to those from the lectotype. Sclerites from these samples generally have larger tubercles and longer marginal spines than those of the lectotype (Fig. 3.18C–D) and the narrower sclerites at the base of the polyps differ from the lectotype as they are rather jagged sclerites with relatively large marginal spines and obvious tubercles (Fig. 3.18Ea) rather than the regularly tuberculate sclerites in the lectotype.

Distribution:

Eastern Antarctic continental shelf; Scotia Arc, Antarctic Peninsula.

Depth:

134–866 metres.

Remarks:

This species is closely related to *P. antarctica,* such that the distinction between the two species is somewhat blurred. The two species both have large, often perpendicular polyps with large, spiny anthopoma and body sclerites. They usually differ in geographic distribution, polyp arrangement, colony form, and coverage of tubercles and marginal spines on the sclerites. However, these distinctions can overlap making designations difficult. In fact, the two species may be a species complex with many smaller units within, but currently the distinguishing factors do not permit easy delineations of some specimens.

The most significant differences between *P. fragilis* and *P. antarctica* are the colony form, polyp distribution and sclerite ornamentation. *P. fragilis* colonies tend to have finer branches, with fewer bifurcations. The branches are often longer with crowded polyps especially at the branch tip and the polyps are more frequently angled distad. *P. antarctica,* however, is more robust, with a thick axis, rigid, short branches and sparse, perpendicular polyps. The polyp body sclerites in *P. fragilis* often (but not exclusively) have significantly more developed marginal spines and tubercles than those from *P. antarctica.* Additionally, the polyp body sclerites of *P. fragilis* are more irregularly shaped than those in *P. antarctica,* with larger indentations and somewhat jagged edges. *P. fragilis* appears to be common on the Antarctic continent while *P. antarctica* is found near the subantarctic islands of Prince Edward and Heard Island.

Other *Primnoisis* species in this sub-genus are distinguished from *P. fragilis* by sclerite form and geographic distributions. *P. erymna* n. sp. has large, rounded, robust, heavily tuberculate sclerites in the anthopoma and polyp body while *P. chatham* n. sp. has smaller, regularly serrated polyp body sclerites. Both species are subantarctic or temperate and do not occur on the Antarctic continent.

Other *Primnoisis* species examined here are from the subgenus *Delicatisis* and have delicate colonies, smaller polyps which are consistently tightly curled in towards the axis, smaller sclerites and the presence of narrow rods and spindles in the anthopoma.

***Primnoisis* (*Primnoisis*) *chatham* new species**

(Figs. 3.19–3.23)

Material examined:

Holotype: NIWA 41540, Chatham Rise, New Zealand, RV *Tangaroa,* stn. 153, (TAN0104/153), 42.733–42.738°S, 179.899–179.90°W, depth 990–1076 m, 18th April 2001.

Paratypes: NIWA 91367, Chatham Rise, New Zealand, RV *Tangaroa,* stn. 153, (TAN0104/153), 42.733–42.738°S, 179.899–179.90°W, depth 990–1076 m, 18th April 2001; **NIWA 41541**, Chatham Rise, New Zealand, RV *Tangaroa,* stn. 194, (TAN0104/194), 42.788–42.783°S, 179.997–179.999°W, depth 880–1042 m, 18th April 2001; **NIWA 69891**, Chatham Rise, New Zealand, RV *Tangaroa,* stn. 194, (TAN0104/194), 42.789–42.783°S, 179.997–179.999°W, depth 880–1042 m, 18th April 2001; **NIWA 53173**, Chatham Rise, New Zealand, RV *Tangaroa,* stn. 42, (TAN0905/42), 42.746–42.744°S, 179.924–179.919°W, depth 1051–1129 m, 18th June 2009; **NIWA 53139**, Chatham

Rise, New Zealand, RV *Tangaroa,* stn. 41, (TAN0905/41), 42.745–42.748°S, 179.924–179.924°W, depth 1020–1125 m, 17th June 2009.

Description:

Colony form:

The holotype is a small bottlebrush-shaped colony with an intact holdfast which has incorporated a brown matrix (possibly sponge skeleton) into the calcification (Fig. 3.19A). There is a central axis, 71 mm long, which is damaged at the distal tip and the colony is approximately 40 mm across at the widest point. There are many primary branches which are robust and rigid, emanate at approximately 45–90° from the central axis (Fig. 3.19B), and are between 12–24 mm long although most have damaged tips. Three proximal internodes of the main axis have no branches but the other internodes have 3–5 branches each. The colony tends to have more primary branches on three sides with many of the branches on one side either broken or stunted—the colony may have been growing against something else. There are commonly 1–2 secondary branches per internode but there can be up to five, emanating from all sides. Branching to the 3rd degree is common but there is some evidence of 4th degree branching as well. The few remaining unbroken branches taper to a fine point and some are slightly curved or twisted. The colony is relatively stiff and robust, particularly proximally. There are no anastomoses. Proximally, the colony has numerous, undamaged polyps and intact coenenchyme but distally it is denuded.

In alcohol, the colony has silvery grey internodes, brown to dark cream polyps and golden brown nodes.

Polyps:

Polyps are sparsely and haphazardly dispersed on all sides of the axis and branches with usually about 1.5 mm between polyps, but there can be up to 3 mm (Fig. 3.19B). There are very few polyps on the central axis but on the branches there are between 2–5 polyps per internode. They do not become more crowded toward the branch tips. They are straight, tubular or cylindrical and most are perpendicular to the branches (Fig. 3.19C–E), although some polyps are angled obliquely to the branches particularly distally. At the terminal twigs, a single polyp occurs slightly offset from the tapering tip (Fig. 3.19D). The polyps are 0.87–1.4 mm tall and 0.4–0.65 mm wide at the neck but at the head they widen to 0.6–0.85 mm. There is minimal expansion of the polyp base at the attachment point. Small, probably juvenile, polyps occur sparsely amongst the adult polyps (Fig. 3.19Da). No brooding polyps were found. Most polyps have the tentacles folded over the polyp mouth forming a flat anthopomal region; some are only partly folded in, forming a pyramidal shaped polyp head.

Axis:

In cross-section, the proximal internodes are circular while distally they are square. The only ornamentation on the internodes are low primary ridges, only visible in areas denuded of coenenchyme. On the internodes at the base of the colony, which are 2.5 mm in diameter, there are approximately 40 primary ridges (Fig. 3.19F) while at the distal tip of the central axis the internode is 0.9 mm in diameter with 18 primary ridges. On the central axis internodes are 2.5–5.5 mm long and nodes are 0.3–0.8 mm long. On the branches internodes are 4.5 mm long and the terminal, four-sided twigs taper to a fine tip (Fig. 3.20A). Some of the primary branches have thickened bases, up to 1.9 mm in diameter (most commonly 1.1 mm) which quickly taper to approximately 0.8 mm after the first node.

Sclerites:

The polyps and colony surface are covered in a thin layer of flattened sclerites. The polyp bodies have flat, serrated scales, arranged transversely on the polyp neck and head and obliquely closer to the polyp base (Fig. 3.19C–E). Between the polyp base and anthopomal region there are 11–19 sclerites in irregular series, each sclerite slightly overlapping the one above. There are no differences between the adaxial and abaxial sides of the polyps.

The anthopoma has compound octants consisting of a complex of 5–7 small, longitudinally and obliquely arranged sclerites, effectively locked together (Fig. 3.20B). Sclerites at the distal tip of the octant are mostly small, flat and rectangular to irregularly shaped rods arranged longitudinally, while sclerites at the proximal end of the octants are larger rods, bent spindles and triangles, usually arranged obliquely, with broadened or bent ends (Fig. 3.20C). Many are robust and rounded with some relatively large tubercles on the surface of the sclerites and pronounced edge spines. The length range is 0.08–0.37 mm.

Tentacles have a crowded row of curved, crescent-shaped scales, arranged transversely (Fig. 3.20D) which have a size range of 0.06–0.16 mm. Those at the proximal end are slightly bigger with minor tubercles and those at the distal end are smaller and more irregular with few or no tubercles.

The polyp body sclerites are mostly rectangular scales with regularly serrated edges and sparse tubercles (Fig. 3.21). The sclerites do not seem to be arranged by size on the polyp with some of the largest sclerites evident on the middle of the polyp body and smaller sclerites both above and below (Fig. 3.19C–E). This species is unusual for this genus in that the polyp body sclerites at 0.1–0.36 mm long are smaller and more delicate than some of the anthopoma sclerites.

The coenenchyme sclerites are small, flattened scales and rods with central tubercles and some edge spines although these are usually only small (Fig. 3.22). They lie longitudinally to haphazardly along the branches, being more jumbled around the polyps and bifurcations. They are 0.07–0.17 mm long.

Variability:

Most of the paratypes consist of multiple fragments of colonies, many of which are denuded of polyps and coenenchyme. Nevertheless, the fragments are similar to the holotype with stiff, robust branches and sparse, perpendicular polyps (Fig. 3.23A, B). In the paratype NIWA 53139, the sclerites differ slightly from those of the holotype—the anthopomal sclerites are flatter and not as robust, with many more square scales rather than narrow tuberculate rods (Fig. 3.23C), and the polyp body sclerites are smaller and smoother with more regularly serrated edges (Fig. 3.23D).

Distribution:

Chatham Rise seamounts, east of New Zealand.

Depth:

880–1129 metres.

Remarks:

Colony form, polyp distribution and polyp shape of this species are all very similar to *P. antarctica* and *P. erymna* n. sp. The preponderance of smaller, serrated polyp body sclerites in *P. chatham* n. sp. distinguishes it from *P. antarctica* which has large, rectangular body sclerites with small marginal spines and *P. erymna* n. sp. which has rounded, heavily tuberculate spindles. *P. fragilis* also belongs in this subgenus but has more crowded polyps, flexible colonies and heavily tuberculate and jagged-looking polyp body sclerites. Additionally, *P. chatham* n. sp. has large, robust, rounded rods and bent spindles in the anthopoma, similar to *P. erymna* n. sp. but different to the flat, lightly tuberculate scales more common in the anthopomas from *P. antarctica* and *P. fragilis.*
P. chatham n. sp. appears to be geographically restricted to the Chatham Rise seamounts of New Zealand with one specimen of *P. erymna* n. sp. being the only other *Primnoisis* species recorded from these sites. Three *P. chatham* n. sp. specimens which were successfully sequenced in this study differed from *P. fragilis* specimens by only 2 nucleotides and had no differences at all from *P. erymna* n. sp. Thus there is much similarity between *P. chatham* n. sp. and *P. erymna* n. sp., and the species delineation depends heavily on the shape and ornamentation of the polyp body sclerites.

Etymology:

The name is taken from the Chatham Rise, east of New Zealand which is the locality of all known specimens of this species.

***Primnoisis* (*Primnoisis*) *erymna* new species**

(Figs. 3.24–3.27)

Material examined:

Holotype: NIWA 39826, Macquarie Ridge, south west of New Zealand, Southern Ocean, NIWA RV *Tangaroa,* stn. 38, (TAN0803/38), 50.097°S, 163.474°E, depth 1070–1123 m, 1st April 2008.

Paratypes: NIWA 91366 & **NIWA 39863 (part)**, same data as holotype; **NIWA 39607**, Macquarie Ridge, south west of New Zealand, Southern Ocean, NIWA RV *Tangaroa,* stn. 19, (TAN0803/19), 48.532°S, 164.948°E, depth 1060–1112 m, 30th March 2008; **NIWA 25395**, Chatham Rise, New Zealand, RV *Tangaroa,* stn. 27, (TAN0604/27), 42.761°S, 179.971°W, depth 757–1095 m, 30th May 2006.

Description:

Colony form:

The holotype is a small, rigid, sparsely bushy colony with a central axis and lateral branches which have a tendency to be more common on two opposite sides making the colony slightly laterally compressed (Fig. 3.24A). The holdfast is missing and the distal half of the colony is denuded of polyps and coenenchyme. It is approximately 70 mm tall and 40 mm at the widest point and the central axis is present for two thirds of this height at which point it divides into four branches. Primary branches emanate from the central axis at wide angles of greater than 45° and ramification to the third degree continues throughout the colony (Fig. 3.24B, C). There are between 1–4 primary branches per internode of the central axis and 1–2, occasionally 3, secondary branches per internode. Primary and secondary branches range in length from 8–24 mm and are approximately 0.5 mm thick proximally, tapering to 0.1 mm at the twigs. Secondary and tertiary branches grow in all directions giving the colony a bushy appearance; however, those which grow perpendicular to the general colony plane are usually relatively short. The whole colony is quite rigid and brittle with little flexibility. There are no anastomoses.

In alcohol the polyps are brown, the internodes a silvery grey and the internodes light golden brown with iridescent edges.

The polyps remaining are in good condition as is the coenenchyme near the polyps. The distal and proximal parts of the colony are denuded.

Polyps:

Polyps are tubular or cylindrical and stand perpendicular to the axes with little or no curvature in the polyp (Fig. 3.24D–F; 3.25A). They are arranged haphazardly on all sides of the axes and are not crowded with 1.5–2.5 mm between them. The central axis has a similar frequency of polyps as to the branches at between 0–3 polyps per internode. The polyps are 0.7–1.6 mm tall, with the polyp head between 0.64–0.9 mm in diameter with a slight indentation for a polyp neck. There is no consistent widening of the polyp base at attachment point. The tentacles fold over the oral area giving the polyp heads a rounded summit with eight indentations between the tentacles. There are some brooding polyps which are smaller, tubular polyps with a single width throughout (no necks or expanded polyp heads) and a pyramidal summit (Fig. 3.24Ea). There are rare juvenile polyps as well.

Axis:

The internodes are essentially circular in cross-section proximally in the colony, but gradually change to square in cross-section at the branch twigs (Fig. 3.25B, C). On the widest internodes there are 16 low, primary ridges while the node 0.6 mm in diameter has 14 primary ridges. These ridges are usually straight, running parallel along an internode but some twist around the internode. Other than the ridges, the internodes are without ornamentation. On the central axis internodes are between 1.5–4.6 mm long and grade from 0.9 mm in diameter in the basal internodes to 0.6 mm in diameter at the point the central axis branches into four branches. Nodes on the central axis are 0.25–0.4 mm long. The primary branches have internodes which are approximately 3 mm long, 0.4 mm in diameter near the bifurcation and taper to a fine tip as twigs approximately 0.1 mm in diameter. The axis and branches are robust and stiff.

Sclerites:

A thin layer of sclerites cover the polyps and colony surface. Polyps have sclerites in approximately 10–12 irregular series with those closer to the polyp head arranged transversely while those sclerites closer to the base are arranged obliquely (Fig. 3.24D–F; 3.25A). There is little or no difference between the abaxial and adaxial sides of the polyp as the polyps are almost all perpendicular to the branches.

The anthopoma consists of complex octants, each made up of 4–6 sclerites, all arranged longitudinally or obliquely (Fig. 3.25D). Those sclerites at the distal tip of the octant tend to be a combination of smaller and irregularly shaped scales and narrow, robust rods all with pronounced tubercles and some obvious edge spines (Fig. 3.26A). The narrower sclerites align along the edge of the anthopoma. Proximally in the octant, the sclerites tend to be triangles (Fig. 3.26Aa) and almost right-angled spindles (Fig. 3.26Ab); these are particularly robust and have well-developed tubercles. All anthopomal sclerites are between 0.1–0.33 mm long.

The tentacles have a row of sclerites which are relatively regular, crescent-shaped scales with toothed edges concentrated in the proximal end of the tentacles, and small, irregular sclerites with protrusions and indentations from the distal tips of the tentacles (Fig. 3.26B). They have very few tubercles and are 0.04–0.15 mm long.

The sclerites from the polyp body are robust, tuberculate scales and spindles, slightly curved to fit the curvature of the polyp body (Fig. 3.27A). Those from near the polyp head tend to be slightly flattened scales, closer to the traditional scales present in *Primnoisis* specimens, but these are few in number. Most of them are rounded spindles with well-developed tubercles, regular edge spines and some minor root processes. They decrease only slightly in length closer to the base of the polyp, with most being from 0.25–0.4 mm long. They are between 0.06–0.16 mm high and have an average height to length ratio of 0.28.

Coenenchyme sclerites are small, slightly flattened, tubercles scales and rods (Fig. 3.27B). They tend to be arranged longitudinally along the branches although this varies around polyps and bifurcation points. Lengths are mostly 0.06–0.2 mm with no obvious differential placement by length.

Variability:

There is good congruence between the samples included in colony and sclerite form.

Distribution:

Three of the samples are from two isolated hauls on Macquarie Ridge, south of New Zealand and one specimen was collected from Chatham Rise, east of New Zealand.

Depth:

757–1123 metres.

Remarks:

In colony form, polyp distribution and polyp shape this species is very similar to *P. antarctica* and *P. chatham* n. sp. However, the polyp body sclerites in *P. erymna* n. sp. (robust, rounded spindles with substantial warts and tubercles) are significantly different to the flat, serrated scales found in *P. chatham* n. sp. and the flat, smooth scales on the polyp bodies of *P. antarctica. P. fragilis* has crowded, curved polyps with flexible colonies and lacks the rounded spindles of *P. erymna* n. sp. All other *Primnoisis* species are from the other subgenus group *Delicatisis* and these have fine, tightly curled, smaller polyps, delicate colonies and smaller sclerites.

Three specimens here assigned to *P. erymna* n. sp. are geographically isolated from other *Primnoisis* species but one specimen was collected on the Chatham Rise, east of New Zealand, along with specimens of *P. chatham* n. sp. These *P. chatham* n. sp. specimens and the single specimen of *P. erymna* n. sp. from Chatham Rise had identical sequences for the two gene regions assessed here. However, these gene regions appear to have low variability within this subgenus *P.* (*Primnoisis*) and further knowledge of gene regions or additional specimens would improve this species designation.

Etymology:

From the latin adjective *erymnos*, fortified or strong, in recognition of the robust nature of the polyp sclerites relative to other *Primnoisis* species.

***Primnoisis* (*Delicatisis*) new subgenus**

Diagnosis:

As for the genus, except colonies are usually delicate with fine branches; polyps small and goblet-shaped, usually tightly curved and at an acute angle to the branch; polyp body sclerites tend to be small, narrow scales or flattened spindles with minimal to extensive tuberculate coverage; anthopomal sclerites are commonly narrow, tuberculate rods and irregular triangular shapes.

Etymology:

In recognition of the delicate nature of the colonies included, the name is derived from the Latin *delicatus*, and combined with *Isis*.

Type Species:

Primnoisis formosa Gravier, 1913 by designation.

***Primnoisis* (*Delicatisis*) *rigida* Wright & Studer, 1889**

(Figs. 3.28–3.31)

Primnoisis rigida Wright & Studer, 1889: 37–38, Pl. VIII Figs. 3, 3a, Pl. 9 Fig. 8; Kükenthal 1915: 123; Kükenthal 1919: 615–616; Kükenthal 1924: 435; Deichmann 1936: 251; Bayer 1959: 30; Pasternak 1993: 4; Alderslade 1998: 263.

Material examined:

Syntypes: NHMUK 1932.12.8.8, colony portion and microscope slide, off the Rio de la Plata, Argentina, HMS *Challenger,* stn. 320, 37.283°S, 53.867°W, depth 1097 m, 14th Feb 1876; **NHMUK 1889.5.27.27a & b**, twigs mounted on microscope slides; **MCZ 90401**, slide of sclerites from syntype NHMUK 1932.12.8.8.

Description:

Colony form:

There are two syntype lots, both stored at NHMUK, and both samples consist of many colony portions and broken pieces (Fig. 3.28A, B). Unfortunately, the piece of the lot NHMUK 1889.5.27.27 sent for examination in this study was the small Primnoidae colony arrowed on Fig. 3.28A. However, given that the remainder of the lot appears to be bushy isidid colonies (Fig. 3.28A) and two original microscope slides examined from this lot have polyps of *Primnoisis* with sclerites which correspond to the other syntype, it remains as a syntype of *P. rigida*. The rest of this description is based on syntype NHMUK 1932.12.8.8, of which some material was made available for examination.

It is impossible to be certain but the syntype lot appears to consist of several fragmented colonies rather than pieces of one single colony (Fig. 3.28B). Many of the pieces are tangled together with the colony form mainly obscured but in general each colony piece seems to have a main stem with many side branches creating bushy, irregularly bottlebrush colony forms. The portion examined lacks a stem, having instead a few slender branches which were probably part of a branch of a larger colony (Fig. 3.28C). The specimen is long, about 110 mm, and narrow, approximately 30 mm at its widest point.

The piece is extensively branched with branching to the fifth degree common, reaching a maximum of the ninth degree. There are anastomoses evident, particularly proximally, making the ramification sometimes difficult to determine (Fig. 3.28D). There are usually 0–4 primary branches per internode which emanate at an angle of approximately 45° from the colony and then tend to curve dorsally and extend basically parallel to the colony (Fig. 3.28E). This means the specimen is relatively narrow with secondary branches similarly curving back in towards their parent then growing loosely parallel which makes many of the branch junctions U-shaped. This branching form makes the specimen quite compact and very bushy, particularly distally. Many of the distal branches are denuded and remnants of a sponge are evident amongst the branches (Fig. 3.28F).

The higher level ramification consists of thin, short, brittle twigs with tapering tips. Wright and Studer (1889) mention again a tendency for the colony to be branched “more particularly in one plane… The largest branches arise from two opposite sides and spread themselves out in the same plane, while the other branches remain shorter.” This was not obvious in the portion examined here; however it does have one side of the colony which is bare of projecting tips with all branches curving away giving the impression this colony has grown against something, but considering the other colony portions in the syntype lot, this branching tendency does not appear to be consistent. There are pieces of sponge and a worm tube growing on and tangled through some of the branches and proximally there are a significant number of denuded portions. In general, the specimen is in good condition with many polyps and much coenenchyme remaining.

Polyps:

Other than where effected by epiphytes and the barer side of the specimen, polyps are spread throughout the colony in a relatively regular fashion. On the main branches of the fragment, the polyps and the coenenchyme are absent but on the proximal branches the polyps occur at 1–5 per internode and up to 7 per internode on the distal twigs and, although Wright & Studer claimed them to be "on the larger twigs and branches mostly on three sides, on the terminal twigs only on one side" they are actually on all sides. The polyps are tightly curved over so occasionally the polyp head touches the branch but the polyp body does not (Fig. 3.29A–C). The base and head of each polyp have approximately similar diameters (0.5–0.65 mm) while the narrower neck region is approximately 0.26–0.6 mm wide giving the polyp a club shape. Polyps are 0.9–1.1 mm long on the adaxial side, and the tentacles are often partly extended (Fig. 3.29C). Almost all polyps have two or three eggs visible in the base. Juvenile polyps are present but rare.

Axis:

The internodes have primary ridges but are otherwise without ornamentation. In the proximal, thicker branches the internodes are essentially circular in cross-section (Fig. 3.29D) with 12 very indistinct primary ridges on an internode 0.8 mm in diameter and 6 primary ridges on an internode 0.6 mm diameter. In the twigs, they are approximately square in cross-section with four primary ridges at the corners (Fig. 3.29E). In the thicker branches the internodes are 6.3–8 mm long and up to 0.8 mm in diameter and in the minor branches they are of similar length although slightly narrower at 0.5 mm in diameter. Wright & Studer stated that the colony in its original condition had internodes up to 18 mm long in the distal branches and that some twigs and lateral branches did not have any nodes making the colony quite brittle and rigid. They also mentioned that the internodes were often "bent and twisted".

Sclerites:

The polyps and branch surface are covered in a single layer of small, fine, translucent sclerites. The anthopoma is symmetrical and each octant is composed of 5–7 small sclerites arranged obliquely or longitudinally (Fig. 3.30A–C). Sclerites in the distal tips of the anthopoma tend to be narrow, tuberculate rods (Fig. 3.31Aa). Proximal anthopomal sclerites are irregularly shaped, slightly flattened sclerites, all with small, consistently sized tubercles (Fig. 3.31Ab). All anthopomal sclerites are approximately 0.12–0.21 mm long.

Tentacles have small, arched scales with a serrated distal edge and few small tubercles (Fig. 3.31B). They are arranged transversely in a single row and are 0.07–0.12 mm long.

Polyp body sclerites are chiefly narrow, slightly curved scales with small, consistently sized, scattered tubercles (Fig. 3.31C) and are arranged transversely in 12–22 irregular series (Fig. 3.30A, D). They are approximately 0.2–0.3 mm long and 0.065–0.12 mm wide with a width to length ratio of 0.34. The width of scales appears to increase distad while the scales at the base of polyp can be quite narrow and tend to transition to coenenchyme sclerites. There are a few pronounced spines on the distal margins, and small root-like projections on the proximal margins on some of the sclerites, but more frequently the sclerites have irregular margins.

Wright & Studer (1889) described the polyps as having "eight regular vertical rows of broad, flat, strong scales, convex in accordance with the periphery of the polyp, strongly toothed and covered with pointed warts….The scales lie upon a support of bent, thorny spindles of 0.08 mm length which form eight longitudinal rows". This description is ambiguous with the mention of both vertical and longitudinal rows of sclerites and my examination of the available material has failed to clarify it. Rows of small (0.08 mm) bent spindles are certainly not evident. In general, the polyps have 12–22 irregular, horizontal rows of sclerites, depending on the size of the polyp, and these do not form definable longitudinal rows.

In the genus description, Wright & Studer (1889: 34–35) stated that "the mesenterial folds are in great part so filled with calcareous spicules that these remain well preserved and rigid even in dried specimens", and also "the spicules in the mesenterial folds are very small, calcareous rodlets, which lie close together and fill the mesoderm of the folds". The syntype portion of *P. rigida* was specifically examined for this and no sclerites were found in the mesenterial folds (Fig. 3.30E, F). In fact, not a single *Primnoisis* specimen examined during the course of this research had any sclerites in the mesenterial folds. It is difficult to know why Wright and Studer included these remarks.

The branch coenenchymal sclerites are small, narrow, slightly flattened rods and spindles with small tubercles and low serrations on the margins (Fig. 3.31D). There are also a few crosses and forked sclerites.

Distribution:

off the Rio de la Plata, Argentina.

Depth:

1097 metres.

Remarks:

The syntypes are the only confirmed specimens of *P. rigida.* No other specimens were available from the vicinity of the type locality and, given the distribution of other species in subantarctic and temperate waters, it is likely that its distribution is limited to that area.

It is distinguished from other *Primnoisis* species by the highly complex and crowded colony with many branches with high-level branching, common anastomoses and narrow polyp body sclerites with low, consistently sized and shaped tubercles.

***Primnoisis* (*Delicatisis*) *delicatula* (Hickson, 1907)**

(Figs. 3.32–3.36)

Ceratoisis (Primnoisis) delicatula Hickson, 1907: 6–7, Pl. II Figs. 13–15.

Primnoisis delicatula Gravier 1914: 9; Kükenthal 1915: 123; Kükenthal 1919: 615; Kükenthal 1924: 431; Thomson & Rennet 1931 [part]: 13, Pl. VIII Fig. 1; Alderslade 1998: 263, Fig. 202.

Material examined:

Syntype: NHMUK 1907-06-12-001, fragment, Winter Quarters (WQ). No. 12 hole, 100 yards south of Hut Point, McMurdo Sound, Antarctica, *Discovery* Expedition, 77.9°S, 166.68°E, depth 46–55 m, 8th Sept 1903; **NHMUK 1961.3.9.151**, slide of syntype, partly dissolved polyp; **NHMUK 1961.3.9.152**, slide of syntype, branch fragment.

Other material: MNHN CE-1854 (part), Dumont d'Urville, Antarctica, RV *L'Astrolabe*, REVOLTA, REVO_37-209, 66.654°S, 139.868°E, depth 107–105 m, 1st Feb 2011.

Material found to be incorrectly determined:

AM G.13235, Commonwealth Bay, Adelie Land, Antarctica, Australian Antarctic Expedition, stn. 2, 66.9°S, 145.4°E, depth 582 m, 28th Dec 1913 => *P. gracilis*.

Description:

Colony form:

Hickson's (1907) description is based on "specimens…[which] are in the form of a tangled mass [of] delicate branches", thus it is not clear if there was originally more than one colony present. The type lot (NHMUK 1907-06-12-001) is thus considered a syntype, possibly consisting of multiple fragmented colonies. There is reportedly minimal material remaining of the syntype lot (Alderslade pers. comm.). All that was available for examination in the present study were two original permanent microslides; one of a piece of twig with 12 intact polyps and one with a polyp partly dissolved. Both slides have deteriorated somewhat, with discolouring of the fixing media and for NHMUK 1961.3.9.151 (the partly dissolved polyp) particularly, apparent desiccation of the fixing medium and clumping of the sclerites such that it is impossible to examine the sclerites individually. However, Alderslade (1998) briefly examined the syntype NHMUK 1907-06-12-001 with resulting photographs reproduced here.

Hickson described the specimens as a tangle of delicate branches and twigs with no attachment points and no "main stems". The branching was described as "irregular and in all directions". The original diagram depicts a colony with sparse branching from the internodes, with ramification only to the second degree (Hickson, 1907, Pl. II, Fig. 11 here reproduced at Fig. 3.32A). There are very few branches per internode (between 0–2 only) although the internodes are difficult to determine on the figure. The delicate branches as illustrated emanate at approximately 45° from a parent branch (Hickson mentioned it as "an acute angle") and most extend to the top of the colony. Colour of the colony cannot be determined from the discoloured slides but photographs of the syntype in alcohol (Fig. 3.32C) show the internodes and polyps to be white and the nodes to be yellowy-brown. Hickson did not specify any colour.

Polyps:

The colony figure depicts polyps arranged irregularly along the branches with approximately 1–3 polyps per internode proximally and more crowded distally although this was not specified by Hickson. He claimed some indication of clumping of polyps with 1–2 mm between polyps within clumps. The slide NHMUK 1961.3.9.152 has a piece of twig (16 mm long) with 12 polyps regularly situated along it with 7 polyps on the single intact internode (Fig. 3.32B). There is evidence that there were more polyps on the twig originally making them quite crowded.

The polyps are club-shaped and usually curved distally with only an indistinct narrowing at the neck (Fig. 3.32B–E). Hickson specified that the polyps are "bent at an acute angle to the axis; the outside measurement is about 0.65 mm". Polyps available here were between 0.45 mm and 1.1 mm on the abaxial side with head diameter of 0.3–0.6 mm. The polyps examined and photographed by Alderslade 1998 appear small and squat, and the sclerites appear very narrow and crowded (Fig. 3.32C–E). However, most of the polyps on the slide NHMUK 1961.3.9.152 are considerably larger, with sclerites which do not usually overlap to such a degree and are not as narrow (Fig. 3.32B). This may be a factor of size and simply that the remaining polyps available for examination by Alderslade were very small. The tentacles are folded over the mouth so the summit of the polyp is rounded. There are some possibly juvenile polyps on the mounted twig (Fig. 3.32B).

Axis:

The internodes are four-sided in cross-section in the mounted twig and in Alderslade's figure (Fig. 3.33A, B) with a primary ridge on each corner and shallow longitudinal groove on each side. They are otherwise without ornamentation. Hickson described the diameter of the thickest stem to be 0.65 mm at the nodes and 0.6 mm at the internodes while the terminal branches are 0.3 mm in diameter and "attenuate distally to a very fine point". Internodes were described by Hickson to be a "fairly constant" 6 mm long.

Sclerites:

The polyps on the slide NHMUK 1961.3.9.152 are mostly in good condition and the sclerites can be viewed with reasonable clarity, as can the sclerites in the coenenchyme. The polyps and branch surface are covered in a thin, transparent layer of sclerites. On the abaxial side of the polyp there is a series of between 16–24 narrow, transversely arranged sclerites from the polyp base to the anthopoma. These do not overlap, or only very slightly overlap, adjacent sclerites (Fig. 3.33E). As the polyps are often angled distally, sclerites on the adaxial side appear slightly more crowded compared with those on the abaxial side. The polyps and coenenchyme both have a prickly appearance due to substantial tuberculation of the crowded sclerites (Fig. 3.32C–E).

The anthopoma is symmetrical and composed of a complex of 5–7 small sclerites arranged longitudinally to obliquely in each octant (Fig. 3.33C, D). Many of these sclerites are small, narrow, tuberculate rods (Fig. 3.34A), some with irregular spines, and these usually lie along the distal edges of the octants (Fig. 3.33C). The proximal area of the octants commonly has irregularly shaped sclerites (Fig. 3.34Aa). Anthopomal sclerites range from 0.07–0.2 mm long. Some irregularly triangular sclerites form the transition between the longitudinal anthopoma sclerites and the transverse polyp body sclerites (Fig. 3.34Ab).

It was not possible to closely examine the arrangement of the sclerites in the tentacles but they appear to have a single row of crescent-shaped sclerites, arranged transversely. These sclerites have a few small tubercles on the flat surface and margins and are 0.07–0.12 mm long (Fig. 3.34B).

Polyp body sclerites are almost exclusively narrow to very narrow scales with pronounced, rounded tubercles (Fig. 3.34C). Some have sharp and irregular spines around their distal margin and some have small roots on the proximal margin. Those from close to the base of the polyp could be considered spindles rather than scales. Each polyp body sclerite is a relatively consistent width with no significant central indentation, meaning sometimes the original orientation of the sclerite is not obvious. Polyp body sclerites range from 0.175–0.25 mm long and 0.045-0.07 mm wide with an average width to length ratio of 0.276.

The surface of the branches have a single layer of often crowded sclerites which are small, narrow rods, scales and spindles with moderate to extensive tubercles (Fig. 3.35A) giving the coenenchyme a prickly or rough appearance. Many are slightly flattened but there are some which have very well-developed tubercles on all surfaces (Fig. 3.35Aa). Alderslade (1998: 263) also notes the "coenenchymal sclerites are very thorny" and depicts them in place (Fig. 3.35B). They are 0.09–0.19 mm long.

Variability:

The only specimen which could be confidently assigned to *P. delicatula* has a tangled colony without an obvious central stem with minimal branching as described by Hickson for the syntype (Fig. 3.36A). Small polyps are arranged almost alternately along the long internodes and are curved distally (Fig. 3.36B). There is a range of size of polyps throughout the colony, with the large polyps being a similar size to those from the slide of the syntype (Fig. 3.36C *cf.* Fig. 3.32B). The smallest polyp in Fig. 3.36C resembles those photographed by Alderslade (Fig. 3.35C–E) although the sclerites do not appear as crowded or as narrow. In general, the sclerites match those of the syntype, with narrow, straight rods and irregularly shaped sclerites in the anthopoma (Fig. 3.36D), simple crescent shaped scales from the tentacles (Fig. 3.36E) and mostly straight, small polyp body sclerites with sharp, irregular marginal spines and relatively large tubercles (Fig. 3.36F). This sample lot, MNHN CE-1854, also had bottlebrush-shaped colonies with a clear central stem and with longer, narrower polyp body sclerites–these have been assigned to *P. formosa.*

Distribution:

Eastern Antarctica—Ross Sea and Dumont d'Urville.

Depth:

46–447 metres.

Remarks

Hickson's description of a tangled mass with no obvious stem is not the bottlebrush-shaped colony common in *Primnoisis* specimens. The specimen assigned here similarly lacks a true bottlebrush growth form. Without a complete colony, the full colony form of *P. delicatula* cannot be confirmed but it appears likely to have long, fine branches with minimal branching.

The main distinguishing features of *P. delicatula* are distally curved polyps, narrow, small, tuberculate body sclerites with sharp, irregular marginal spines, numerous narrow, tuberculate rods in the anthopoma and very delicate colonies with a tangled, bushy colony form with long internodes. Polyps appear to be uniformly distributed without crowding.

There is much similarity between *P. delicatula* and *P. formosa*, which was originally collected from the entrance to Marguerite Bay, between Jenny Island and Adélaïde Island on the Antarctic Peninsula. The polyps and sclerites of the two species have similar shapes and appearance; however the main difference between the species is colony form (bottle-brush for *P. formosa*) and the length and width of the body sclerites, with the *P. formosa* holotype having longer and narrower polyp body sclerites than *P. delicatula* and slightly smaller, less obvious tubercles and more regular marginal spines. Many specimens from the same geographic areas as *P. delicatula* are here assigned to *P. formosa* but some with a degree of uncertainty. Sequences obtained here from the recently collected *P. delicatula* specimen differ from those from *P. formosa* specimens by only a single nucleotide. Future work, including genetic research, on colonies from the peninsula area may find *P. delicatula* and *P. formosa* are synonymous.

The polyp form is also similar to *P. niwa* n. sp. but can be distinguished by the more irregular, sharply defined marginal spines on the polyp body sclerites of *P. delicatula* in contrast to *P. niwa* n. sp. which has sclerites with rounded, consistently-shaped, tubercules on the margins. *P. gracilis* is distinguished from *P. delicatula* by having wider body sclerites with an indented central proximal margin and crowded polyps, particularly near branch tips. *P. millerae* n. sp. has wide polyp body sclerites with a consistent cover of regular tubercles and distinct bottlebrush-shaped colonies.

***Primnoisis* (*Delicatisis*) *formosa* Gravier, 1913**

(Figs. 3.37–3.42)

Primnoisis formosa Gravier, 1913: 453; 1914: 31–34, Pl. I. Figs. 3–5, textfigs. 21–26; Kükenthal 1915: 123; 1919: 617; 1924: 436; Molander 1929: 79; Grant 1976: 38–39, Figs. 33–35

Material examined:

Holotype: **MNHN OCTO-221**, entrance to Marguerite Bay, between Jenny Island and Adelaide Island, Antarctica, 2nd Expedition Antarctique Francaise 1908-1910, dragage VI, 67.75°S, 68.55°W, depth 254 m, 15th Jan 1909; **?Paratype MNHN OCTO-223**, Marguerite Bay, Antarctica, 2nd Expedition Antarctique Francaise 1908-1910, dragage VIII, 70.2°S, 78.2°W, depth 176 m, 20th Jan 1909.

Other material: ZMB 5460, *P. fragilis* syntype, Gaußstation, Antarctica, Deutche sudpolar-expedition 1901-1903, approximately 66.03°S, 89.63°E, depth 350–385 m, 12th Jan 1903; **ZMB 5453**, determined as *P. antarctica* by Kükenthal (1912), Gauss Station, Antarctica, Deutche Sudpolar Expedition 1901–1903, depth 385 m, 24th Jan 1903; **AM G.13204**, (part) determined as *P. fragilis* in Thomson & Rennet (1931), Commonwealth Bay, Adelie Land, Antarctica, Australian Antarctic Expedition, stn. 1–D, 66.833°S, 142.1°E, depth 640 m, 22nd Dec 1913; **AM G.13225**, determined as *P. ambigua* in Thomson & Rennet (1931), Davis Sea, off Shackleton Iceshelf, Antarctica, Australian Antarctic Expedition, stn. 8, 66.1°S, 94.3°E, depth 219 m, 27th Jan 1914; **AM G.13233**, Commonwealth Bay, Adelie Land, Antarctica, Australian Antarctic Expedition, stn. 1–C, 66.833°S, 142.1°E, depth 101 m, 21st Dec 1913; **SAM H.17948**, off Vincennes Bay, Knox Coast, Antarctica, BANZARE, stn. 98, 65.117°S, 107.483°E, depth 502 m, 27th Jan 1931; **NIWA 41524**, Sabrina Island, Balleny Islands, Antarctica, NZOI, stn. E215a, 66.503°S, 162.417°E, depth 190 m, Feb 1965; **NIWA 41555**, Sabrina Island, Balleny Islands, Antarctica, NZOI, stn. E0224, 66.519°S, 162.450°E, depth 199 m, 12th Feb 1965; **NIWA 35749**, (part), Ross Sea, Antarctica, RV *Tangaroa,* TAN0802 stn. 31, 74.591°S, 170.276°E, depth 283 m, 11th Feb 2008; **NIWA 36776**, Ross Sea, Antarctica, RV *Tangaroa,* TAN0802 stn. 94, 74.193°S, 176.296°E, depth 447 m, 17th Feb 2008; **TMAG K4299**, Commonwealth Bay, Terra Adelie, Antarctica, CEAMARC 26A–436, 66.517–66.532°S, 140.001–140.047°E, depth 176–262 m, 13th Jan 2008; **TMAG K4297** & **K4298**, Tressler Bank, Shackleton Iceshelf, Antarctica, RV *Aurora Australis,* V2 East Antarctica, stn. BTC07, 64.284–64.283°S, 97.120–97.109°E, depth 637–709 m, 2nd Jan 2010; **TMAG K4296**, Shelf break canyon, Wilhelm II Land, Antarctica, RV *Aurora Australis,* V2 East Antarctica, stn. BTC30, 65.836–65.834°S, 89.541–89.544°E, depth 547–502 m, 8th Jan 2010; **MNHN CE-0629**, Dumont d'Urville, Antarctica, RV *L'Astrolabe*, REVOLTA, REVO_133-133, 66.618°S, 140.000–140.004°E, depth 107–103 m, 11th Jan 2011; **MNHN CE-1535**, Dumont d'Urville, Antarctica, RV *L'Astrolabe*, REVOLTA, REVO_09-187, 66.668°S, 139.827°E, depth 132–129 m, 27th Jan 2011; **MNHN CE-1621**, Dumont d'Urville, Antarctica, RV *L'Astrolabe*, REVOLTA, REVO_55-201, 66.623°S, 139.969–139.970°E, depth 116–117 m, 31st Jan 2011; **MNHN CE-1854 (part)**, Dumont d'Urville, Antarctica, RV *L'Astrolabe*, REVOLTA, REVO_37-209, 66.654°S, 139.868°E, depth 107–105 m, 1st Feb 2011.

Description:

Colony form:

The holotype is a bottlebrush-shaped colony with a single stem, two main primary branches more bulky and longer (70–80 mm long) than others which lie basically parallel to the main axis and many short lateral branches on all sides (Fig. 3.37A). The holdfast is missing but otherwise the colony appears intact and in good condition. Total length is 230 mm and at the widest point the colony is

40 mm across. The stem is 1.5 mm in diameter at the base and tapers to 0.6 mm distally. From the stem, primary branches emanate from internodes at an angle of about 45–90° (Fig. 3.37C); usually there are 3–5 branches per internode but it can be as few as one or up to seven (Fig. 3.37B). Gravier (1914) claimed there can be twelve to fifteen branches per internode but this appears to be an error. Most of the lateral branches are a consistent length of about 30 mm with minimal secondary branching. The consistent length of these branches gives the colony a regular width and a simple bottlebrush-like structure. The two primary branches have multiple secondary and some tertiary branches, and up to four branches per internode. The colony does not look crowded due to the slender nature of the branches and relatively short primary branches. All the branches are fine (proximally 0.6 mm tapering to 0.3 mm in diameter) and reasonably flexible, as is the whole colony. The internodes are white, nodes dark brown and the polyps light cream.

Polyps:

The polyps occur on all branches and the stem, and on all sides. Distribution of the polyps is loosely alternate with approximately 0.5–1 mm space between them (Fig. 3.37D). There are up to four polyps per internode on the central stem but this number increases on the lateral branches to usually 8–12 polyps per internode. Gravier described at least 20 polyps per centimetre on the secondary and tertiary branches. Although there are many polyps they do not appear crowded as they are small at 0.5–0.8 mm long on the abaxial side and 0.35–0.48 mm wide at the polyp head. There is an obvious neck region, slightly narrower than the polyp head, and the polyp base is a similar diameter to the polyp head (Fig. 3.37D, E). The polyps never overlap or touch and are strongly curved upwards, with the polyp head curved around towards, but rarely touching, the branch. There is no significant difference between the adaxial and abaxial sides of the polyp, although commonly the sclerites are more crowded on the adaxial side. The tentacles are almost always contracted into the oral region and the polyp summit is slightly rounded to flat. There are brooding polyps present which are straight sided with a dome-shaped head with no clear anthopoma arrangement—those pictured are from the extra material examined and resemble those from the holotype (Fig. 3.38A). They are a similar size to the non-brooding polyps and each carry a single egg.

Axis:

The proximal internodes, which are circular in cross-section, have 8–12 low, distinct, primary ridges. These ridges decrease in number further up the colony, eventually becoming four corner ridges on the delicate internodes on the terminal twigs which are square in cross-section (Fig. 3.38B). Other than the ridges, the internodes are without ornamentation. On both the stem and the lateral branches internodes are usually 3.5–5.5 mm long, although there are a few very short internodes of less than 2.5 mm and one up to 6 mm long. Nodes are 0.3–0.6 mm long.

Sclerites:

The polyps and colony surface are all covered in a thin, transparent layer of sclerites. Polyp body sclerites are arranged transversely in 11–16 irregular series which tend to slightly overlap the sclerite above.

The anthopoma consists of complex octants, each made up of an array of 5–7 small sclerites which are arranged obliquely or *en chevron* at the proximal end, often slightly overlapping, and longitudinally at the octant tip (Fig. 3.38C), with a similar arrangement in the extra material examined (Fig. 3.38D). The sclerites are short, narrow, tuberculate rods and irregularly shaped sclerites, some with broadened or spiked ends (Fig. 3.38E). The narrow rods are slightly smaller at 0.09–0.16 mm long while the irregular shapes are up to 0.21mm long.

The tentacles have a single row of transversely arranged, gently curved, crescentic scales with little or no tubercles (Fig. 3.38F). They are 0.05–0.095 mm long.

Polyp body sclerites are long, very narrow, tuberculate scales and spindles (Fig. 3.39A). Those occurring distally on the polyp are widest while those from close to the base of the polyp are generally narrower and grade from scales to spindles. The distal margin of the sclerites usually has slightly more developed spines and tubercles than the proximal margin, and some sclerites have root-like extensions of the proximal margin (Fig. 3.39Aa, b). Simple tubercles occur throughout on most sclerites, and can be sparse or crowded. The sclerites are 0.19–0.36 mm long and 0.046–0.1 mm wide giving an average width to length ratio of 0.247.

Coenenchymal sclerites are mostly small tuberculate rods ranging from 0.06–0.24 mm long (Fig. 3.39B), some of which are very narrow and have substantial tubercules. They form a single layer of sclerites over the internodes and nodes, and are mostly arranged longitudinally along the axis.

Variability:

Paratype MNHN OCTO-223 has a similar colony form to the holotype, with a central main stem and bottlebrush-like branching (Fig. 3.40A, B) and was collected close to the type location. However the sclerites differ from the holotype as follows: the anthopomal sclerites are smaller with fewer tubercles (Fig. 3.40C) and the polyp body sclerites are generally wider with well-developed root-like projections and very low, small tubercules (Fig. 3.40E). These differences could be general variability but as no other specimens from this geographic area were available this could not be assessed. None of the other material examined resembled this paratype so it has been included here as an uncertain determination.

The remaining samples are delicate, simple bottlebrush-shaped colonies, although many with longer lateral branches than the holotype. They all have small, distally curved polyps arranged relatively regularly along the branches, being almost alternate in places. The colony MNHN CE-1535 has many polyps with their tentacles partly extended making the top of the polyps pyramidal, and the polyps are bigger (up to 1 mm on the abaxial side) and more substantial than those of the holotype, with sclerites appearing less crowded (Fig. 3.41A–C). Similarly, TMAG K4297 has larger polyps with less densely crowded sclerites (Fig. 3.42A, B). The anthopomas of the additional colonies have small, narrow rods longitudinally arranged distad in the anthopoma, and more irregularly shaped sclerites arranged obliquely in the proximal area (Fig. 3.42C), similar to the holotype, as are the sclerites with the short, tuberculate rods common in the anthopoma (Figs. 3.41D; 3.42D), simple crescentic tentacle sclerites (Figs. 3.41E; 3.42E) and long, narrow, extensively tuberculate body sclerites (Figs. 3.41F; 3.42F). Coenenchyme sclerites generally also resemble those from the holotype (Fig. 3.42G).

Distribution:

Marguerite Bay, Antarctic Peninsula and eastern Antarctica including Dumont d'Urville, Shackleton Iceshelf, Commonwealth Bay and the Ross Sea.

Depth:

101–709 metres.

Remarks:

Gravier stated at the end of his description that this species is clearly distinguished from all other species then described. Unfortunately, he did not specify what he thought clearly defined *P. formosa,* and this deficiency combined with the minimal descriptions for the other nominal species has meant this species has remained poorly differentiated.

The distinguishing features are here considered to be the regularity of branching giving a simple bottlebrush colony form, the semi-regular distribution of polyps, and the narrow, long, tuberculate body sclerites. Additionally the polyps are usually smaller than other species but not exclusively. The polyp body sclerites are very similar to those of *P. delicatula,* although they are longer and narrower in *P. formosa.* These species also differ in colony form, with *P. delicatula* having very long, tangled branches and no central stem—however the difference between these species is slight. They occur sympatrically on the Antarctic continent and are very closely related genetically (see section 3.3.3). *P. gracilis* also occurs sympatrically with *P. formosa* but differs by having wider polyp body sclerites, many with a central indentation on the proximal margin, and crowded polyps, particularly on the distal twigs. *P. formosa* is similar to *P. niwa* n. sp. and *P. millerae* n. sp. in colony form but has smaller, more tightly curved polyps, and narrower body sclerites with more irregularly distributed and sized tubercles than these species. These species are also clearly differentiated genetically (see section 3.3.3) and geographically (Chapter 4).

P. formosa appears to be relatively common on the Antarctic continental shelf with extensive colonies recently collected from eastern Antarctica. The current distribution for this species is disjointed, with the holotype from the Antarctic Peninsula and the rest of the specimens from eastern Antarctica. Further research in areas between these disjunct sites would allow a more robust distribution pattern, including confirmation of a possible circumpolar distribution.

***Primnoisis* (*Delicatisis*) *gracilis* (Gravier, 1913) new combination**

(Figs. 3.43–3.48)

Mopsea gracilis Gravier, 1913a: 454; 1913b: 1470; 1914: 38–43, Pl. VI. Figs. 26–27, textfigs. 39–51; Kükenthal 1915: 124; 1919: 626; 1924: 441; Molander 1929: 80; Bayer & Stefani 1987: 944.

Primnoisis? Alderslade 1998: 263.

Material examined:

Holotype: **MNHN OCT-213**, entrance to Marguerite Bay, between Jenny Island and Adélaïde Island, Antarctica, Antarctique Francaise 1908-1910, dragage VI, 67.75°S, 68.55°W, depth 254 m, 15th Jan 1909; **Paratype MNHN OCT-214**, data as for holotype.

Other material: AM G.13204 (part), determined as *P. fragilis* by Thomson & Rennet (1931), Commonwealth Bay, Adelie Land, Antarctica, Australian Antarctic Expedition, stn. 1–D, 66.833°S, 142.1°E, depth 640 m, 22nd Dec 1913; **AM G.13223**, determined as *P. ambigua* by Thomson & Rennet (1931), Commonwealth Bay, Adelie Land, Antarctica, Australian Antarctic Expedition, stn. 1–D, 66.833°S, 142.1°E, depth 640 m, 22nd Dec 1913; **AM G.13224** & **G.13248**, determined as *P. ambigua* by Thomson & Rennet (1931), Davis Sea, off Shackleton Iceshelf, Antarctica, Australian Antarctic Expedition, stn. 8, 66.1°S, 94.3°E, depth 219 m, 27th Jan 1914; **AM G.13235**, determined as *P. delicatula* by Thomson & Rennet (1931), Commonwealth Bay, Adelie Land, Antarctica, Australian Antarctic Expedition, stn. 2, 66.9°S, 145.4°E, depth 582 m, 28th Dec 1913; **AM G.13280**, determined as *P. sparsa* by Thomson & Rennet (1931), Commonwealth Bay, Adelie Land, Antarctica, Australian Antarctic Expedition, stn. 2, 66.9°S, 145.4°E, depth 582 m, 28th Dec 1913; **SAM H.17939**, Prydz Bay, Antarctica, RV *Aurora Australia*, stn. 40, 67.017°S, 78.193°E, depth 266–251 m, 17th Feb 1991; **SAM H.17940**, Prydz Bay, Antarctica, RV *Aurora Australia*, stn. 41, 67.51°S, 77.238°E, depth 333–341 m, 18th Feb 1991; **MNHN IK-2009-0285**, Commonwealth Bay, Terra Adelie, Antarctica, CEAMARC, stn. 027–045, 66.017°S, 142.7167°E, depth 421–463 m, 23rd Dec 2007; **MNHN IK-2009-0358**, Commonwealth Bay, Terra Adelie, Antarctica, CEAMARC, stn. 042–167, 66.883°S, 142.65°E, depth 262–431 m, 28th Dec 2007; **MNHN IK-2009-0297**, Commonwealth Bay, Terra Adelie, Antarctica, CEAMARC, stn. 063–314, 65.833°S, 142.983°E, depth 423–433 m, 4th Jan 2008; **MNHN IK-2009-0323**, Commonwealth Bay, Terra Adelie, Antarctica, CEAMARC, stn. 022–503, 66.017°S, 139.333°E, depth 466–485 m, 15th Jan 2008; **TMAG K4300**, Commonwealth Bay, Terra Adelie, Antarctica, CEAMARC, stn. 002–416, 66.001–66.0°S, 141.354–141.299°E, depth 229–232 m, 12th Jan 2008; **TMAG K4301**, Commonwealth Bay, Terra Adelie, Antarctica, CEAMARC, stn. 017–485, 66.169–66.175°S, 139.932–139.99°E, depth 150–151 m, 15th Jan 2008; **TMAG K4302**, Shelf break canyon, Wilhelm II Land, Antarctica, RV *Aurora Australia,* V2 East Antarctica, stn. BTC25, 65.866–65.866°S, 89.281–89.260°E, depth 540–537 m, 6th Jan 2010; **TMAG K4303**, Shelf break canyon, Wilhelm II Land, Antarctica, RV *Aurora Australia,* V2 East Antarctica, stn. BTC29, 65.867–65.868°S, 89.033–89.036°E, depth 561–587 m, 8th Jan 2010; **NIWA 36001**, Ross Sea, Antarctica, RV *Tangaroa*, TAN0802 stn. 46, 74.737°S, 167.061°E, depth 863–866 m, 13th Feb 2008; **MV F173636**, Fram Bank, Prydz Bay, Antarctica, RV *Aurora Australia,* ANARE AA97, stn. 16, 67.138–67.141°S, 70.646–70.647°E, depth 293 m, 4th Mar 1997; **MV F173639**, Fram Bank, Prydz Bay, Antarctica, RV *Aurora Australia,* ANARE AA97, stn. 17, 67.166°S, 70.666°E, depth 290 m, 5th Mar 1997; **MV F173634 (part)**, central Prydz Channel, Prydz Bay, Antarctica, RV *Aurora Australia,* ANARE AA97, stn. 11, 67.188–67.190°S, 70.294–70.304°E, depth 544 m, 22nd Feb 1997; **USNM 99141**, Queen Maud Land, Coats Land, Off Halley Bay, Weddell Sea, Antarctica, RV *Polarstern*, EPOS 3, stn. 230, 75.237°S, 26.99°W, depth 270 m, 30th Jan 1989.

Description:

Colony form:

The paratype MNHN OCT-214 is here described in parallel with the holotype due to limited access to the holotype and minimal material remaining of both specimens. There is good congruence between the two specimens.

The holotype now consists of two extremely delicate colony fragments with few undamaged polyps remaining. These fragments can be matched to Gravier's figure (Fig. 3.43A cf. B). Although Gravier stated that the colony is planar there was so little material that he could be simply describing a fragment of a larger, not planar colony. He acknowledged he had several colonies of this species available but all were incomplete. The holotype was described as 6 cm in height and 6.5 cm wide. There is one slender main branch, with a diameter of 0.53 mm proximally and 0.35 mm distally, and very sparse secondary branching from that, with no or one branch per internode (Fig. 3.43A, B). All branching is from the internodes. These branches emanate at approximately 45° in a single plane as mentioned by Gravier and are similarly sparsely branched. Most of them have broken tips. All secondary branches and twigs are slender and delicate with diameters of approximately 0.3 mm.

Paratype MNHN OCTO-214 is similarly fragile with minimal material available (Fig. 3.43F). However, branching on the fragments available appears also to be sparse and the internodes are of similar diameters and lengths to the holotype.

The internodes are white, the nodes are golden brown and the polyps are beige to cream.

Polyps:

Many of the polyps from the holotype have been dislodged or damaged but Gravier figured and described the polyps as being very crowded, particularly on the branch tips, with little space between them (Fig. 3.43C). On the central branch there are 9–12 polyps per internode although there is evidence they were more crowded than this on the twigs. Gravier stated they were distributed on all sides of the branches. They are all acutely curved upwards with the polyp head often just touching the branch (Fig. 3.43D, E). They are generally clavate with a distinct neck region which is markedly narrower than the large, rounded polyp head. Polyps are 0.7–0.9 mm long on the abaxial side and polyp heads are between 0.4–0.8 mm in diameter. This corresponds to Gravier's estimate of no more than 1 mm in height. The tentacles are tightly folded into the oral region and each polyp has a rounded summit. Mixed among these are brooding polyps which lack most of these characteristics and instead have straight sides and a domed summit, and thus are lacking a neck, a distinguishable polyp head and an anthopoma. These are usually filled with a single large egg.

Polyps on the paratype are not quite as rounded, and do not curve as much as those on the holotype (Fig. 3.43G, H). However, there were very few polyps available for examination so this may not be consistent. A few juvenile polyps are present on the paratype.

Axis:

The internodes have low, primary ridges but are otherwise without ornamentation—proximally the internodes are essentially circular in cross-section with 8–12 low primary ridges, distally the internodes become square in cross-section with four indistinct corner ridges. On the central axis, the internodes are 4–7 mm long and 0.3–0.5 mm in diameter. On the branches, the internodes are 3.5–4.5 mm in length but Gravier described them as being up to 6 mm long. Nodes are between 0.15–0.25 mm long.

Sclerites:

Polyps and parts of the colony surface are covered in a thin, transparent layer of sclerites; the remaining parts are denuded. There are approximately 12–18 irregular series of transversely arranged sclerites on the abaxial side of each polyp although the arrangement is often very indistinct. Most polyp body sclerites slightly overlap the one above.

Sclerites from the holotype and paratype MNHN OCTO-214 were found to have good congruence and figures of both are included here due to the limited material of the holotype. In both colonies, the anthopoma has complex octants which are comprised of 6–8 small sclerites arranged longitudinally to obliquely (Fig. 3.44A). Many of these sclerites are small, narrow rods with small tubercles but there are also many irregular shapes with lateral processes, indentations and some with broadened ends (Figs. 3.44B; 3.45A). In the holotype the anthopomal sclerites are 0.06–0.15 mm long and those in the paratype are a similar length at 0.05–0.16 mm.

In both colonies, the tentacles have a single row of crescent shaped, narrow scales with very few tubercles (Figs. 3.44C; 3.45B). All the margins have small indentations and there is little difference between the aboral or oral edges. They are usually between 0.044–0.11 mm long in both specimens.

The distal polyp body sclerites in both type specimens are smooth scales with flattened marginal processes (Figs. 3.44D; 3.45C), often with blunt peaks (Figs. 3.44Da; 3.45Ca). Many have a central indentation on the proximal margin and there are a few small tubercles on the sclerite surface. These sclerites occur distad on the polyp and continue some of the way down the polyp body. Proximally, the sclerites tend to be narrower with more regular, rounded tubercles on their margins (Figs. 3.44Db; 3.45Cb) and tend to lack the proximal, central indentation. In the holotype, polyp body sclerites range in length from 0.11–0.25 mm long but the width varies slightly more, with distal sclerites ranging from 0.06–0.09 mm in width while the proximal sclerites are 0.03–0.07 mm wide. This gives an overall average width to length ratio of 0.375. The polyp body sclerites from the paratype are a very similar length at 0.14–0.25 mm and width (distal sclerites from 0.06–0.1 mm wide and proximal sclerites from 0.03–0.05 mm).

In both specimens, coenenchyme sclerites are slightly flattened rods (Fig. 3.45D, E), 0.038–0.2 mm long, with simple tubercles. Some larger ones resemble the proximal body sclerites, with a likely mixing of these sclerites at the point of polyp attachment.

Variability:

Many additional recently collected colonies from East Antarctica have been determined here as *P. gracilis.* Colony form varies, with some large colonies having a single main stem, denuded of lateral branches proximally and many crowded, delicate, flexible branches bunched distally, while in others, collected at the same site, the branches are not as crowded (Fig. 3.46A). There are other colonies with very crowded polyps, especially distally, with long, flexible branches but without the long stem (Fig. 3.46D, E). Other bottlebrush-shaped colonies have relatively sparsely distributed branches (Fig. 3.46G). Polyps are arranged irregularly on all sides of the branches, tightly curved upwards, and are often so crowded as to be often touching (Fig. 3.46B–C, E–F), although in other cases the polyps are well separated (Fig. 3.46H, I). Anastomoses are common amongst the distal twigs of many colonies (Fig. 3.46E). Despite the variability in colony form and polyp distribution, the colonies pictured all have similar sclerites and were found to have identical molecular sequences (see section 3.3.3).

Similar to the type specimens, TMAG K4303 has a complex anthopoma consisting of numerous small sclerites arranged longitudinally or obliquely (Fig. 3.47A).

The anthopomal and polyp body sclerites found in all the East Antarctic samples and one sample from the Weddell Sea are more jagged and spinous than those from the type specimens (Figs. 3.47B–G; 3.48A–F). Compared to the latter, the scales are far more tuberculated and the marginal processes are longer and sharper resulting in deeper marginal indentations. Additionally, the extra material has much more extensively tuberculate polyp body sclerites present at the base of the polyps than those of the type specimens (Fig. 3.48Fa). The coenenchyme sclerites of specimen TMAG K4301 are similarly more tuberculate than those from either of the type specimens (Fig. 3.47G). These differences may be a function of the poor state of the type specimens and that the only remaining polyps are relatively small.

Distribution:

Antarctica: Marguerite Bay, Weddell Sea, Commonwealth Bay, Prydz Bay, Shackleton Iceshelf.

Depth:

150–866 metres.

Remarks:

Alderslade (1998), during a revision of the genus *Mopsea,* examined the holotype of *Mopsea gracilis* Gravier, 1913 and noted that it had an anthopoma similar to that of *Primnoisis*. Considering that Gravier (1914) described *Primnoisis formosa* Gravier, 1913 and included *P. antarctica* specimens in the same paper it is surprising that he did not equate the *M. gracilis* specimen with them. However, at the time planar versus bottlebrush growth form was the dominant characteristic separating *Mopsea* and *Primnoisis* and as this small fragment was essentially planar, perhaps this is the reason Gravier assigned it to *Mopsea.* As the specimen has a complex anthopoma consisting of numerous sclerites arranged obliquely and longitudinally and has an axis lacking spines it is now reassigned to *Primnoisis.* Given that *Primnoisis* specimens have almost exclusively bottlebrush or bushy colony forms it is feasible to suggest that the *M. gracilis* holotype is a fragment of a larger, bushy colony.

Grouping the recent colonies from East Antarctica with *P. gracilis* (from the Antarctica Peninsula) suggests a disjunct distribution for this species which would be worthy of further investigation. No specimens from the Antarctic Peninsula matching the morphology of *P. gracilis* were available for genetic extraction but the East Antarctic specimens formed a single clade using the gene regions mtMutS and igr1–COI (see section 3.3.3). Future work may allow a genetic comparison with populations from the Antarctic Peninsula. At present there is insufficient reason to erect another species for these geographically distant populations, with the caveat that this morphological assessment is based on minimal material from the peninsula region. The specimen from the Weddell Sea (USNM 99141 Fig. 3.53D–F) has sclerites more closely resembling those from the east Antarctic colonies than those from the geographically closer type species. However, only a fragment of this specimen was available for examination.

The distinguishing characteristics of this species include a bushy, crowded colony form often with a long stem, many long, delicate branches with common anastomoses, crowded, acutely curved polyps, especially at the branch tips, many narrow, tuberculate rods in the anthopoma and wide scales with distinct marginal spines, arranged distally on the polyp. These polyp body sclerites usually have a deep central incision on the proximal edge. Proximally on the polyp, the body sclerites tend to be more regularly shaped and have less jagged margins. Colony form and sclerite shape are most similar to those of *P. mimas* which is distinguished by its relatively large, fleshy polyps, much more numerous small body sclerites and two rows of sclerites in the tentacles.

Gravier (1914) discussed at length bulky growths or galls on his material, which has brooding polyps projecting from them, each with a large egg. In these galls there are also three, sometimes more, parasitic copepods. Gravier described and figured the copepods later in the same paper and mentioned he also found them in the holotype of *P. formosa*.

***Primnoisis* (*Delicatisis*) *millerae* new species**

(Figs. 3.49–3.54)

Material examined:

Holotype: NIWA 65170, Ross Sea, Antarctica, TRIP 2994, stn. 23, 72°S, 179°W, depth 885–1559 m, 5th Jan 2010.

Paratypes: NIWA 65168, Ross Sea, Antarctica, TRIP 2732, stn. 19, 73°S, 179°W, depth 933–745 m, 6th Jan 2009; **NIWA 65172**, Ross Sea, Antarctica, TRIP 2993, stn. 55, 72°S, 177°W, depth 942–895 m, 4th Jan 2010; **NIWA 68568**, Ross Sea, Antarctica, TRIP 2993, stn. 93, 72°S, 179°W, depth 1281–1339 m, 18th Jan 2010; **NIWA 65173**, Ross Sea, Antarctica, TRIP 2995, stn. 33, 71°S, 177°E, depth 1300–1500 m; 30th Dec 2009; **NIWA 65215**, Ross Sea, Antarctica, TRIP 2729, stn. 45, 72°S, 176°E, depth 1274–1455 m, 10th Jan 2009; **NIWA 68565**, no location information; **NIWA 68569**, Ross Sea, Antarctica, TRIP unknown; **AM G.13234,** Bruce Spur, off Queen Mary Land, Antarctica, Australian Antarctic Expedition, stn. 6, 63.2°S, 101.7°E, depth 1591 m, 14th Jan 1914.

Description:

Colony form:

The holotype is a flattened, bushy, fan-shaped colony with many fine, delicate branches spreading more or less in one plane from a short stem (Fig. 3.49A). The colony is approximately 106 mm wide and 125 mm tall, although the base of the colony is broken and the holdfast is missing. The short stem dissipates into many small branches, so numerous it is difficult to determine the ramification, but it appears to be at least to the fifth degree. Most branches emanate at approximately 45° or less and extend to the top of the colony, making it bushy, particularly distally. Although the primary branching is more commonly in one plane, the distal twigs tend to branch in all directions. There are 2–4 branches per internode on the stem and usually only 0–2 per internode on the primary branches, although there are some instances of 4–5 per internode. Primary branches are approximately 50–70 mm long and 0.8–1.2 mm wide at their base but quickly become only 0.5 mm wide, then taper to fine points at the tips. The most distal twig of the branches is often gently curved (Fig. 3.49B) and anastomoses are evident, particularly distally. The colony is in good condition with many polyps and intact coenenchyme on the branches and twigs.

In alcohol, the internodes are silvery white, the polyps are light cream, and the nodes are light golden brown and slightly translucent. The nodes are silvery where they join the internodes.

Polyps:

The small, delicate and mostly translucent polyps are arranged roughly alternate, along all the branches and twigs and on all sides (Fig. 3.49B, C). The proximal internodes of the stem are mostly denuded of coenenchyme but appear to have had very few polyps. There are up to 15 polyps per internode on some of the longest internodes, but more commonly 8–9 polyps per internode on the primary branches. The polyps are never crowded and have a relatively regular space between them of 0.5–1.2 mm. They do not clump at the branch tips but there is usually a single polyp, slightly offset from the tapering tip of the branches (Fig. 3.50A, B). The polyps are clavate, often rounded, and curved upwards (Figs. 3.49C; 3.50A–C), although there are a few polyps directed downwards. The polyps are tightly curved but their head usually does not touch the branch. Most are 0.45–1 mm tall with some taller polyps up to 1.4 mm tall and 0.27–0.38 mm wide at the polyp head. The tentacles are almost all folded tightly into the oral region, making the polyp summit mostly flat or only slightly rounded (Fig. 3.50B, C). Among the adult polyps, there are numerous brooding polyps which are globular with a conical summit (Fig. 3.49Ca). There are also many small, presumably juvenile, polyps.

Axis:

There are low primary ridges on the internodes— these usually run longitudinally but can also partly spiral around (Fig. 3.50D). There are approximately 40 ridges on the proximal internode which is 3 mm wide and an internode 0.8 mm wide has approximately 16 very indistinct ridges. Otherwise the internodes are without ornamentation. Internodes of the short stem are generally 3–6 mm long although one is 9.5 mm. Internodes of the primary and secondary branches are relatively long at 4.5–8.5 mm, and as many of these are fine and only 0.5 mm wide they are easily broken. The distal internodes are square in cross-section with four rounded corners and there are many examples of anastomoses (Fig. 3.50E).

Sclerites:

The polyps and branches are covered in a single layer of sclerites. The polyps have transversely arranged scales in 14–18 indistinct series on the body, each scale slightly overlapping the one above (Fig. 3.50A–C), and a complex of 6–8 small sclerites, arranged obliquely and longitudinally, makes up each anthopomal octant (Fig. 3.50F, G).

The anthopomal sclerites are short, flattened rods, narrow rods, and irregular shapes with broadened ends, all with an extensive cover of tubercles and many with sharp marginal spines (Fig. 3.51A). The wider, irregularly shaped sclerites are placed obliquely in the base of the octant while those at the tip of the octant tend to be narrow rods and are arranged longitudinally. They vary from 0.08–0.21 mm long.

On the tentacles there is a single row of transversely arranged crescent-shaped sclerites (Fig. 3.51B) which are 0.09–0.14 mm long. Many have regularly notched distal margins and some have a few small tubercles on their surface.

The polyp body sclerites are narrow, robust, heavily tuberculate scales (Fig. 3.52A) most of them slightly curved to fit the polyp body and many have pronounced spines on their distal margin. The external face of the larger sclerites has large tubercles, which are of a consistent size and usually occur regularly spaced all over. Some of the smaller sclerites have only small tubercles and do not have an obvious difference between their upper and lower margins. Larger sclerites are 0.2–0.3 mm long and tend to be distad on the polyps, while the proximal sclerites are smaller (0.11–0.2 mm long) with fewer marginal spines and tend to merge with the surface sclerites at the base of the polyp.

Coenenchymal sclerites are arranged mostly longitudinally on the surface and comprise narrow, small, tuberculate spindles and slightly flattened scales that range from 0.06–0.25 mm long (Fig. 3.52B).

Variability:

Some of the paratypes are not fan-shaped; rather they tend to be bushy colonies without the tendency to branch in one plane, but all the branches are fine and numerous making them densely branched like the holotype (Fig. 3.53A–C). However other paratypes are a very similar shape to the holotype (Fig. 3.53D).

The axial internodes are long and fragile, and polyps are arranged semi-regularly and are never crowded. Most colonies have polyps with a distinctive shape reflective of those from the holotype as shown in Fig. 3.50B, with an almost flat summit and a wide polyp head. All colonies have sclerites strongly resembling those of the holotype, with well-developed but regularly sized and distributed tubercles on the external face of the narrow scales from the polyp body, irregular shapes and rods from the anthopoma and simple crescentic scales from the tentacles (Fig. 3.54).

Distribution:

East Antarctic continent including Ross Sea and Commonwealth Bay.

Depth:

745–1591 metres.

Remarks:

Genetically, *P. millerae* n. sp. specimens group inconsistently together but separately from all other clades and are most closely related to *P. niwa* n. sp. (section 3.3.3). Morphologically these species are very similar but can be differentiated on colony form, with *P. millerae* n. sp. having colonies tending to have only a very short stem from which arise many crowded, delicate branches often forming fan-shaped colonies. Polyp body sclerites in *P. niwa* n. sp. are narrower with larger, more crowded marginal spines, often have one long, lateral root-like process and have a less regular cover of tubercles than those of *P. millerae* n. sp. Additionally, the species are separated geographically, with *P. millerae* n. sp. recorded on the eastern Antarctic continent and *P. niwa* n. sp. only recorded on the ridge running north and south of Macquarie Island.

This species also resembles *P. rigida* in that they both exhibit complex branching with fine, long internodes, crowded branching, regularly spaced polyps, and polyp body sclerites with a consistent cover of tubercles on the outer face. Distinctions include different polyp shapes (*P. millerae* n. sp.

has polyps with a flattened, relatively wide polyp head while *P. rigida* polyps have a narrow, pyramidal polyp head), differences in the marginal spines of the polyp body sclerites (sharp marginal spines in *P. rigida* and rounded in *P. millerae* n. sp.), much larger tubercles in *P. millerae* n. sp. and a large geographic distance between the records, including the significant barrier of the Antarctic Circumpolar Current.

This species can be differentiated from the other species in this subgenera by the complex and bushy colony form and the robust, regularly tuberculate polyp body sclerites.

Etymology:

This species is named in honour of Dr Karen Miller, my wonderful PhD supervisor, for the constant encouragement and patience that she has provided to me and her enduring enthusiasm for this thesis.

***Primnoisis* (*Delicatisis*) *niwa* new species**

(Figs. 3.55–3.58)

Material examined:

Holotype: NIWA 41048, Macquarie Ridge, south of Macquarie Island, Southern Ocean, NIWA RV *Tangaroa*, stn. 103 (TAN0803/103), 56.287–56.287°S, 158.451–158.443°E, depth 1170-1420 m, 16th April 2008.

Paratypes: NIWA 46402, Macquarie Ridge, south of Macquarie Island, Southern Ocean, NIWA RV *Tangaroa*, stn. 89 (TAN0803/89), 55.381–55.382°S, 158.427–158.434°E, depth 504–637 m, 15th April 2008; **NIWA 46410** & **NIWA 40949 (part)**, Macquarie Ridge, south of Macquarie Island, Southern Ocean, NIWA RV *Tangaroa*, stn. 98 (TAN0803/98), 56.246–56.242°S, 158.506–158.515°E, depth 676–750 m, 16th April 2008; **NIWA 41002** & **NIWA 40979,** Macquarie Ridge, south of Macquarie Island, Southern Ocean, NIWA RV *Tangaroa*, stn. 102 (TAN0803/102), 56.242–56.242°S, 158.462–158.455°E, depth 790–1025 m, 16th April 2008; **NIWA 40459 (part)**, **NIWA 40461 (part), NIWA 46392** & **NIWA 46394,** Macquarie Ridge, north of Macquarie Island, Southern Ocean, NIWA RV *Tangaroa*, stn. 77 (TAN0803/77), 53.738–53.738°S, 159.114–159.122°E, depth 1014–925 m, 11th April 2008; **NIWA 40634 (part)**, **NIWA 40662 (part), NIWA 46388**, **NIWA 46386** & **NIWA 46399 (part)**, Macquarie Ridge, north of Macquarie Island, Southern Ocean, NIWA RV *Tangaroa*, stn. 84 (TAN0803/84), 53.705–53.705°S, 159.115–159.106°E, depth 998–1100 m, 13th April 2008; **NTM CO12789**, North Macquarie Ridge, north of Macquarie Island, Southern Ocean, CSIRO RV *Southern Surveyor,* stn. 96, (SS199901/96), 53.912°S, 159.032°E, depth 1023 m, 26th Jan 1999; **NTM CO12788**, North Macquarie Ridge, north of Macquarie Island, Southern Ocean, CSIRO RV *Southern Surveyor,* stn. 94, (SS199901/94), 53.93°S, 159.092°E, depth 453 m, 26th Jan 1999; **TMAG K1385**, North

Macquarie Ridge, north of Macquarie Island, Southern Ocean, CSIRO RV *Southern Surveyor,* stn. 94, (SS199901/94), 53.93°S, 159.092°E, depth 453 m, 26th Jan 1999; **unregistered AAD sample**, Macquarie Ridge, north of Macquarie Island, Southern Ocean, 54.007–53.955°S, 158.866–158.888°E, depth 1796 m, 19th July 2009.

Description:

Colony form:

The holotype is a compact, complete, bottlebrush-shaped colony with a small, flat holdfast (Fig. 3.55A). The colony is 89 mm tall and 33 mm at the widest point, decreasing in width distally. There is a tendency for the branches to be more developed on two sides making the colony slightly laterally compressed. The colony is not crowded as the branches are regularly spaced and not profusely divided (Fig. 3.55B). Primary and secondary branches are common but tertiary branches are rare and usually very short. Primary branches emanate from the stem at approximately 45° and there are usually 3–6 branches per internode. Primary branches are approximately 10–30 mm long and 1.2 mm thick proximally tapering to 0.5 mm distally. There are usually 1–4 secondary branches per internode but there is never more than one tertiary branch per internode. Secondary branches are commonly 8–15 mm long although there are some branches which are only 2–5 mm long. Branches taper to a relatively blunt tip with a polyp always slightly offset from the tip. There are no anastomoses.

In alcohol, the polyps are white, the internodes silvery white and the nodes are golden brown and translucent in the centre (Fig. 3.56A). The edges of the nodes where they meet the internodes are iridescent.

Polyps:

Polyps are arranged loosely alternate and are not crowded, even close to the branch tips (Fig. 3.55B), with usually 0.8–1.6 mm between them. They stand out from the branch at an angle of about 35–55° and are gently curved upwards although there are a few polyps directed downwards. The polyp head does not curve around to touch the branch. They are clavate and 0.7–1.2 mm long measured on the abaxial side (Fig. 3.55C–E). The polyp head is approximately 0.55–0.75 mm in diameter and the neck is approximately 0.3–0.47 mm wide. There is from one to rarely three polyps per internode on the stem and 2–5 polyps per internode on the branches. The tentacles fold into the polyp mouth, leaving the polyp summit rounded, although some are flat (Fig. 3.55C–E).

Axis:

Internodes are circular in cross-section at the base of the colony and branches (Fig. 3.56A) and generally grade to square in cross-section at the twigs (Fig. 3.56B), although some of the branch tips are still circular in cross-section and relatively blunt. The proximal internodes of the stem at 1.2 mm wide, have approximately 24 low, longitudinal, primary ridges which decrease to 6 ridges in the distal internodes which are 0.5 mm wide. Other than the ridges, the internodes are without ornamentation. The internodes of the stem usually range between 3.8–9 mm long, mostly increasing in length distally with the few most basal internodes being only 2–2.5 mm long. The nodes of the stem are 0.25–0.7 mm long. The branches usually have a very short stump of axis at the junction before the first node, after which the internodes are approximately 4.5–5.5 mm long and 0.3 mm wide with about 5 primary ridges.

Sclerites:

A thin layer of sclerites covers the polyps and colony surface. There are 12–14 irregular series of transversely arranged sclerites on the adaxial side of the polyps, each sclerite slightly overlapping the one above (Fig. 3.55E). In the anthopoma, octants are complex consisting of 6–8 small sclerites, effectively locked together to form a continuous covering (Fig. 3.56D). Proximally in the octant are irregularly shaped sclerites often arranged obliquely (Fig. 3.56C). These have large tubercles and obvious spines, particularly around the broadened ends and are 0.14–0.18 mm long (Fig. 3.56E). Other sclerites in the octants are narrow, tuberculate rods, many with well-developed spines. These sclerites are usually arranged longitudinally in the octant tip and on the outer edges of the octant, and are 0.09–0.2 mm long.

The tentacles have a single row of transversely arranged, crescent-shaped scales, 0.07–0.13 mm long, many of which have a dentate distal margin (Fig. 3.56F). Some have numerous tubercles on the upper surface but mostly tubercles are sparse.

The polyp body has transversely arranged, narrow, robust, heavily tuberculate, often fusiform scales (Fig. 3.57A), which have a moderate to extensive covering of tubercles and commonly have crowded spines and tubercles on their distal margins (Fig. 3.57Aa). Many have an extended narrow, often smooth, lateral root-like process extending on one side, and some have small irregular root-like projections on the proximal margin. Sclerites are 0.14–0.3 mm long and 0.03–0.11 mm wide giving a width to length ratio of 0.31.

The coenenchyme has small, tuberculate rods (Fig. 3.57B) which are 0.06–0.15 mm long. A few of them are slightly flattened, they all have well-developed tubercles and spines and they are arranged longitudinally to obliquely on the branches and twigs.

Variability:

Many of the colonies are likely to have originally been larger than the holotype but almost all have been damaged in the collection process and are now in many pieces (Fig. 3.58A–C). Larger colonies appear to have longer twigs which tangle and intertwine and these twigs are finer than those in the holotype. One of the colonies from the NIWA 41002 lot has smaller polyp body sclerites with more irregular and less crowded marginal spines on the distal margin compared with those of the holotype and largely lack the single lateral root-like process (Fig. 3.58E). The anthopomal sclerites are also slightly smaller and lack the robust, long rods present in the holotype (Fig. 3.58D). There is also a single, inverted Y-shaped sclerite which is possibly two merged anthopoma sclerites (Fig. 3.58Da) and was probably situated mid-way along an octant.

Distribution:

Macquarie Ridge, north and south of Macquarie Island, Southern Ocean

Depth:

453–1100 metres

Remarks:

The main distinguishing morphological features of this species are: a fine, delicate colony form with widely spaced polyps which are slightly curved upwards, and polyp body sclerites with relatively crowded tubercles and spines, particularly on the distal margins and a lateral, largely smooth, root-like process. This group of specimens form a single molecular clade consistently separate from other specimens (see section 3.3.3). Geographic distance also separates this species from all others from this subgenus with *P. niwa* n. sp. restricted to Macquarie Ridge.

P. millerae n. sp is the species which is most closely related genetically and most similar morphologically, however it has much more crowded branching, and wider, more robust polyp body sclerites which have a covering of consistently spaced tubercles and lack a lateral root-like process. Of the other species within the subgenus, *P. rigida* has very complex, rigid, crowded branching and polyp body sclerites with small tubercles, *P. delicatula* has long, tangled colonies with no central stem, *P. formosa* has longer and narrower body sclerites with sharper marginal spines and *P. gracilis* has many small, crowded polyps arranged along the branches and wide, lightly tuberculate polyp body sclerites. *P. tasmani* n. sp. is also quite similar to *P. niwa* morphologically but has bigger polyps which curve tightly and is much more robust with thicker branches and larger, more irregularly ornamented polyp body sclerites.

Differentiation from these species based on morphological characters alone is difficult so geographical and genetic differences were also needed to confirm this species. Morphological differences viewed in isolation may fail to distinguish this species.

Etymology:

The species is named after the National Institute of Water and Atmospheric Research (NIWA), the premier marine research organisation in New Zealand, in honour of its substantial and ongoing research on deep water corals.

Unplaced to subgenus

Primnoisis ambigua Wright & Studer, 1889

(Figs. 3.59–3.62)

Primnoisis ambigua Wright & Studer, 1889: 39, Pl. IX Fig. 9; Kükenthal 1915: 123; Kükenthal 1919: 615; Kükenthal 1924: 435; Alderslade 1998: 263.

NOT ?*Primnoisis ambigua* Hiles 1899: 196, Pl. XXII Fig. 11 => perhaps *Pteronisis laboutei* (Bayer & Stefani, 1987), only photographs of colony viewed.
NOT *Primnoisis ambigua* Thomson & Rennet 1931: 11.
NOT *Primnoisis ambigua* Grant 1976: 39, Fig. 36 => only photograph of colonies sighted.

Material examined:

Holotype: NHMUK 1889.5.27.30, colony portions, Kerguelen Island, Southern Ocean, HMS *Challenger,* stn not noted, approximately 48.87°S, 70.02°E, 18–146 m, Dec 1873/Jan 1874; **ZMA COEL07447**, fragment of holotype.

Material found to be incorrectly determined:

AM G.13223, determined as *P. ambigua* by Thomson & Rennet (1931), Commonwealth Bay, Adelie Land, Antarctica, Australian Antarctic Expedition, stn. 1–D, 66.833°S, 142.1°E, depth 640 m, 22nd Dec 1913 => *P. gracilis.*

AM G.13248 & G.13224, determined as *P. ambigua* by Thomson & Rennet (1931), Davis Sea, off Shackleton Iceshelf, Antarctica, Australian Antarctic Expedition, stn. 8, 66.1°S, 94.3°E, depth 219 m, 27th Jan 1914 => *P. gracilis.*

AM G.13225, determined as *P. ambigua* in Thomson & Rennet 1931, Davis Sea, off Shackleton Iceshelf, Antarctica, Australian Antarctic Expedition, stn. 8, 66.1°S, 94.3°E, depth 219 m, 27th Jan 1914 => *P. delicatula.*

Description:

Colony form:

The holotype consists of a fan-shaped colony that has two or three primary branches emanating at acute angles from a short stem (Fig. 3.59A) that is missing a holdfast. In general, the colony has a "somewhat bilateral appearance" due to a tendency for stronger branching in one plane (Wright & Studer 1889). The primary branches occasionally bifurcate equally but more commonly a smaller, secondary twig emanates from the primary branches at acute angles of between 25–45° (Fig. 59B–D). Rarely these will have tertiary twigs although Wright & Studer (1889) stated that ramification up to the fourth order was observed in the holotype in its original condition. All branching occurs from the internodes. Many internodes have no or only one branch (there are rarely two branches per internode) but the colony is still somewhat bushy as most of these long, slender branches reach right to the top of the colony.

The colony portions examined here are loosely dichotomous and are almost entirely branched in one plane although terminal twigs can branch outside the plane (Fig. 3.59B–D). The largest portion is approximately 93 mm long and 34 mm at the widest point. At the base the branch is 0.6 mm wide, decreasing in width distally with most terminal twigs tapering to a fine point (Fig. 3.59C). Primary branches in the portions examined are approximately 20–35 mm long but can be up to 60 mm long and have an approximate diameter of 0.4 mm proximally with usually one or no secondary branches per internode. Most of the branch tips are intact but much of the colony surface is denuded of polyps and coenenchyme, these only being present on some of the terminal twigs. Wright & Studer indicated that "the coenenchyma is only preserved in the terminal twigs and some of the larger branches" so this condition appears close to original. The coenenchyme on the twigs is thick and opaque but thins somewhat on the larger branches.

In alcohol the colony has white internodes, brown nodes and yellowish, opaque polyps.

Polyps:

The polyps are completely missing from the base of colony but are reasonably crowded distally (Figs. 3.59D–F). They occur on all sides of the twigs with no discernable arrangement and not in spirals of four as suggested by Wright & Studer. On the primary branches there can be between 7–12 polyps per internode with only 0.5–1 mm between the polyps. On the main branch of one of the colony portions examined, internodes were found to have slightly fewer polyps (3–10 per internode) although one internode had 13 polyps. This supports Wright & Studer who specified that the polyps were more irregularly and sparsely distributed at the base of the twigs and on the primary branches than on the terminal twigs. Polyps are robust and opaque with a rounded head, a slight constriction at the neck and a wide base (Fig. 3.59E, F). They are curved obliquely upwards on the twigs but the heads rarely touch the branch. Adult polyps range in length from 0.5–0.75 mm measured on the adaxial side with head diameters of 0.375–0.55 mm. Almost all of the polyps have the tentacles folded into the mouth forming a flat polyp summit (Fig. 3.59E; 3.60A). Juvenile polyps occur throughout and are a similar shape to the adult polyps, but are smaller at 0.25 mm long and 0.25 mm wide.

Axis:

In the holotype, the short stem and the base of the main branches appear to have very short internodes and proportionally large nodes (Fig. 3.59A). The internodes of the main branches of the largest portion examined have average lengths of 2.5–3.2 mm but on the primary and secondary branches they are more commonly 3–5 mm long. Wright & Studer gave a length range of nodes in the main stem as 0.5–1 mm and the nodes of the distal branches were measured here as 0.3–0.4 mm long. The thick coenenchyme masks the nodes towards the top of the colony. At the base of the largest colony portion, the internodes are essentially circular in cross-section with 14 low primary ridges for an internode 0.6 mm in diameter and 8 ridges on a more distal internode 0.3 mm in diameter (Fig. 3.60B). Side branches and distal twigs are almost all four-sided or square in cross-section (Fig. 3.60C). The primary ridges appear to twist or curve around the internodes. Other than the low ridges the internodes are without ornamentation.

Sclerites:

The polyps and coenenchyme appear prickly and opaque with a covering of many thick, warty, crowded sclerites. There appear to be approximately 12–14 series of transverse sclerites on the adaxial side of the polyp, although the margins of the sclerites are difficult to discern (Fig. 3.60A). The anthopoma is symmetrical and continuous with the polyp body sclerites. Each octant consists of 6–8 sclerites with one or two sclerites arranged transversely at the intersection of the octant and the body sclerites, then obliquely or *en chevron* at the base of the octant and longitudinally at the tip (Fig. 3.60D). The anthopomal sclerites are irregularly shaped scales and rods extensively ornamented with well-developed tubercles and marginal spines (Fig. 3.61A). Most are between 0.11–0.2 mm long. The marginal spines angle in many directions and effectively knit the sclerites together.

The tentacles contain a single row of transversely arranged, crescent-shaped scales, 0.07–0.11 mm long, with small tubercles and irregularly dentate distal margins (Fig. 3.61B).

The polyp body is covered all around by transversely arranged, narrow, slightly curved, thorny scales, which slightly overlap the sclerite above. They are heavily ornamented with irregular, sharp spines and tubercles (Fig. 3.61C). The spines are particularly pronounced on the distal margin and some also have complex root-like structures on the proximal margin. The spines and tubercles are also present on the surface of the sclerites making the sclerites quite rugged and bulky. The scales are 0.115–0.30 mm long and 0.07–0.135 mm wide with an average width to length ratio of 0.45. Sclerites from lower on the polyp body tend to be slightly shorter with smaller spines.

The surface of the branches and twigs contains irregularly shaped spindles and rods, 0.05–0.25 mm long, with short, irregular spines and tubercles (Fig. 3.62). They are robust and prickly and are arranged closely together, longitudinally to obliquely along the branches.

Distribution:

Iles Kerguelen.

Depth:

18–146 metres.

Remarks:

P. ambigua is unusual within the genus of *Primnoisis.* The colony form is not bottlebrush-shaped or very bushy, being almost planar at the colony base with minimal, almost dichotomous branching although it becomes slightly more complex distally in the colony. Additionally, the sclerites are more complex than other *Primnoisis* species with projecting tubercules and warts making the polyps and coenenchyme thick and opaque. The arrangement of the sclerites on the polyps is difficult to observe due to the complex, crowded sclerites. The species is very like specimens of *Notisis* Gravier, 1913 with similar polyp body and coenenchyme sclerites and a similarly complex anthopoma consisting of sclerites arranged longitudinally to obliquely. However, specimens of *Notisis* have a single row of low spines on the primary ridges of the internodes (although these may be reduced or absent in the oldest portions of a colony) and have a more strictly planar growth form (Alderslade 1998). Additionally, *Notisis* species have two, slightly overlapping rows of crescent-shaped sclerites in each tentacle while most *Primnoisis* species have only a single row per tentacle. The tentacles of the *P. ambigua* holotype were examined carefully, and appear to have only one row of sclerites per tentacle, however the size and tightly contracted state of the polyps made this very difficult to determine. No other specimens of *P. ambigua* were located amongst the collections examined here, which included two extensive collections from around Heard Island, close to the type location. It is conceivable this is an anomalous specimen from either genus with an apt name.

Primnoisis mimas **Bayer & Stefani, 1987**

(Figs. 3.63–3.66)

Primnoisis mimas Bayer & Stefani, 1987: 947, Figs. 3c, 3d, 5, 6.

Material examined:

Holotype: USNM 78356, fragment, vicinity of South Georgia Island, Scotia Sea, USARP, RV *Islas Orcadas,* cruise 575, stn. 101, 54.235°S, 37.903°W, depth 164–183 m, 10th June 1975; **Paratype USNM 78357,** fragment, same data as holotype.

Other material: USNM 84377, fragment, Shag Rocks, South Georgia Island, RV *Professor Siedlecki,* cruise 86–01, stn. 7, 53.45°S, 42.05°W, depth 159–183 m, 30th Nov 1986.

Description:

Only a tiny fragment of the each of the specimens was available to be examined so colony form is based on the original descriptions. Bayer & Stefani stated that the holotype is a 43 cm tall, bottlebrush-shaped colony with up to three branches from each internode of the main axis and their photograph is reproduced here (Fig. 3.63A). The branches all emanate from internodes, are directed upwards and are up to 7 cm long. They form a crowded bunch at the top of the colony and most of the short, proximal internodes of the stem lack branches.

Polyps:

The fragment of the holotype examined here is an apical twig with distally curved polyps, which are tightly crowded and overlapping each other (Fig. 3.63B, C). There are 9–11 clavate polyps per internode with no space between them. The polyps are very large and fleshy compared with other *Primnoisis* species and are 1.2–2.2 mm tall on the abaxial side, 0.9–1.2 mm in diameter at the polyp head and 0.45–0.6 mm in diameter at the polyp neck or base. Many have their very fleshy tentacles partly extended making the polyp summit a rounded mound (Fig. 3.63C–F).

Axis:

All the internodes are “sculptured with distinct longitudinal ridges and grooves” (Bayer & Stefani 1987) but otherwise lack ornamentation. Mid-section internodes of the stem reach 4–4.5 mm long decreasing distally and the internodes of the branches “average 2.5 mm in length”. The stem and branches are approximately 0.7 mm in diameter and the branches taper to 0.3 mm at the distal twigs.

Sclerites:

The polyps and colony surface are covered in a single layer of sclerites. On the polyps, sclerites are arranged transversely, slightly overlapping the sclerite above, with 18–24 irregular series on the abaxial side (Fig. 3.63D).

The anthopoma has octants which consist of a complex array of 12–18 narrow scales, effectively locked together to form an armoured surface (Figs. 3.63E, F; 3.64A–C). At the base of the octant, the sclerites are arranged obliquely and up to four abreast. At the distal tip of the octant sclerites are in irregular *chevrons* and the transition to the tentacle sclerites is often obscure (Fig. 3.64B, C).

Anthopomal sclerites are irregular, tuberculate scales and rods, some with broadened ends and pronounced marginal spines (Fig. 3.65A) and are between 0.1–0.24 mm. There are some smaller, somewhat triangular sclerites (Fig. 3.65Aa) which lie at the transition point between the transverse polyp body sclerites and the obliquely arranged anthopomal sclerites.

Bayer & Stefani’s figures and description appear to erroneously depict the anthopomal sclerites as crescent-shaped scales arranged transversely and they describe “smaller, transversely placed, scales with more closely serrated margins [which] extend along the back of the tentacles, curved to fit the contour of the tentacle rachis”. They seem to have been describing the tentacle sclerites rather than those from the anthopoma, but if so failed to note the nature of the anthopomal sclerites.

Each tentacle has two slightly overlapping rows of crescentic scales, arranged obliquely at the transition with the anthopomal sclerites and grading to transversely at the tip of the tentacle (Figs. 3.63F; 3.64C, D). The sclerites have few tubercles, slightly dentate margins and can be irregularly shaped; they are 0.1–0.18 mm long (Fig. 3.65B). Bayer & Stefani describe some tentacle sclerites which have a slightly splayed end and “show a peculiar twist” and which they thought extended into the pinnules. While sclerites matching this description were not found, some tentacle sclerites with a slightly splayed end appeared to be arranged with the splayed end oriented at the apex of the tentacle rachis where the ends of the two adjacent tentacle sclerites sometimes met.

Polyp body sclerites are slightly curved scales with pronounced marginal spines and indentations (Fig. 3.65C). Many of them are quite irregular and some have patches of significantly developed and crowded spines making parts of the sclerites complex (Fig. 3.65Ca). A central indentation on the proximal margin occurs on some sclerites but most of the sclerites are quite irregularly shaped—more irregular than those polyp body sclerites pictured by Bayer & Stefani (1987: Fig. 6c). It is often difficult to determine the original orientation of some of the scales as there is little consistency in the form of the proximal and distal margins. The scales are 0.18–0.27 mm long and approximately 0.05–0.12 mm wide giving an average width to length ratio of 0.39.

Coenenchymal sclerites are small, tuberculate, flattened rods (Fig. 3.66A), lying mostly longitudinal along the branch but the polyps are so close together on the fragments examined that the arrangement of these sclerites is largely obscured. The sclerites measured here are 0.07–0.2 mm long but Bayer & Stefani recorded coenenchyme sclerites between 0.25–0.3 mm long. They also described the sclerites as “distinctly flattened and scale like”.

Variability:

The paratype fragment examined is very similar to the holotype with crowded, large polyps, fleshy tentacles, up to 26 transverse series of polyp body sclerites and anthopomal octants with numerous obliquely arranged sclerites (Fig. 3.66B, C). However, some polyps on the paratype appear to have much smaller polyp body sclerites that are opaque and lie obliquely adjacent rather than transversely overlapping (Fig. 3.66D) and make these particular polyps look quite different from others on the fragment. The features of the fragment from USNM 84377 correspond to those in the holotype.

Distribution:

South Georgia Island.

Depth:

159–183 metres.

Remarks:

As well as the description of *P. mimas,* Bayer & Stefani provided a discussion of the position and status of the nominal species of *Primnoisis*. They recognised that some of the species were inadequately delineated but despite this were compelled to erect *P. mimas* to accommodate specimens which were so clearly different from the existing *Primnoisis* species. Chief among these differences is the size, robustness and fleshiness of the polyps and tentacles, the large number of series of polyp body sclerites, 12–18 sclerites per octant and two rows of sclerites in each tentacle. All other *Primnoisis* species have polyps which are delicate, almost transparent and considerably smaller than those from *P. mimas*, usually have <20 transverse body sclerites, only 5–8 sclerites per octant and a single row of sclerites in each tentacle. *P. mimas* has crowded, tightly curved polyps like those species in the subgenus *P.* (*Delicatisis*) but has large scales dominant in the anthopoma like those species in *P.* (*Primnoisis*). Thus it is unplaced to subgenus and possibly should not even remain in *Primnoisis* but further research, including genetic assessments is required to confirm its position.

The species most resembles *P. gracilis* which also has large, bottlebrush-shaped colonies with the branches bunched in a crowded mass at the colony crown, crowded polyps, and polyp body sclerites with central indentations on their proximal margins and pronounced marginal spines. However, the number of sclerites in the octants and the number of rows of sclerites in the tentacles clearly delineate these species.

Within-colony variation was mentioned by Bayer and Stefani and, even in the tiny fragments examined here, was found to be significant. The paratype fragment has some polyps with the common arrangement for *Primnoisis* specimens—transparent, overlapping large polyp body scales (Fig. 3.66C)—but there are also some polyps with rounded, smaller, whitened sclerites which do not overlap, and are arranged haphazardly (Fig. 3.66D). These polyps do not seem to have the extensive modifications usually encountered in brooding polyps but perhaps the sclerite variation is an artefact of past brooding. More extensive examination of the whole colony is required to assess the magnitude and significance of the within-colony variation of this paratype.

***Primnoisis tasmani* new species**

(Figs. 3.67–3.74)

Material examined:

Holotype: TMAG K4275, Main Pedra seamount, west of Huon Commonwealth Marine Reserve (CMR), SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor,* stn. 23, sample 25 (SS200702/023-025), 44.261–44.266°S, 147.097–147.092°E, depth 730–1000 m, 2nd April 2007.

Paratypes: TMAG K4276, same data as holotype; **TMAG K4025**, Z16 seamount, west of Huon CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor,* stn. 22, sample 38 (SS200702/022-038), 44.292–44.294°S, 147.067–147.065°E, depth 1100–1300 m, 2nd April 2007; **TMAG K4027**, Tasman 1200 seamount, Tasman Fracture CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor,* stn. 39, sample 15 (SS200702/039-015), 44.135–44.140°S, 146.150–146.141°E, depth 1130–1180 m, 5th April 2007; **TMAG K4029**, Tasman 1000 slope, Huon CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor,* stn. 9, sample 16 (SS200702/009-016), 44.154–44.162°S, 147.128–147.131°E, depth 800–920 m, 31st March 2007; **TMAG K4030**, Tasman 1000 slope, Tasman Fracture CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor,* stn. 41, sample 41 (SS200702/041-041), 44.066–44.074°S, 146.234–146.224°E, depth 800–880 m, 5th April 2007; **TMAG K4031**, Tasman 1200 slope, Tasman Fracture CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor,* stn. 50, sample 3 (SS200702/050-003), 44.201–44.187°S, 146.199–146.210°E, depth 1050–

1230 m, 6th April 2007; **TMAG K4032**, Huon 1000 seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor,* stn. 10, sample 56 (SS200702/010-056), 44.154–44.164°S, 147.129–147.132°E, depth 800–950 m, 31st March 2007; **TMAG K4033**, Huon 1000 slope, Huon CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor,* stn. 27, sample 6 (SS200702/027-006), 44.126–44.133°S, 147.248–147.248°E, depth 800–1000 m, 3rd April 2007; **TMAG K4034**, Main Pedra seamount, west of Huon CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor,* stn. 11, sample 14 (SS200702/011-014), 44.260–44.266°S, 147.097–147.092°E, depth 730–1000 m, 31st March 2007; **TMAG K4035**, Huon 1000 slope, Huon CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor,* stn. 59, sample 48 (SS200702/059-048), 44.069–44.081°S, 147.423–147.419°E, depth 810–1020 m, 7th April 2007; **TMAG K4277**, Hill U seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor,* stn. 13, sample 46 (SS200702/013-046), 44.327–44.329°S, 147.179–147.179°E, depth 1200 m, 1st April 2007; **TMAG K4278**, Main Pedra seamount, west of Huon CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor,* stn. 18, sample 6 (SS200702/018-006), 44.259–44.257°S, 147.093–147.086°E, depth 850–1000 m, 2nd April 2007; **TMAG K4153**, K1 seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor*, stn. 28 (SS199701/28), 44.293–44.297°S, 147.412–147.337°E, depth 1252–2136 m, 25th Jan 1997; **TMAG K4154**, J1 seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor*, stn. 37 (SS199701/37), 44.272–44.215°S, 147.325–147.397°E, depth 1004–1537 m, 27th Jan 1997; **TMAG K4155**, J1 seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor*, stn. 40 (SS199701/40), 44.243–44.273°S, 147.36–147.323°E, depth 1024–1548 m, 27th Jan 1997; **TMAG K4156**, Dory Hill seamount, west of Huon CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor*, stn. 49 (SS199701/49), 44.322–44.34°S, 147.115–147.072°E, depth 1167 m, 29th Jan 1997; **TMAG K4157**, Mackas seamount, west of Huon CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor*, stn. 52 (SS199701/52), 44.212–44.222°S, 147.045–147.052°E, depth 1084 m, 29th Jan 1997; **TMAG K4158**, Andy's Hill, west of Huon CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor*, stn. 56 (SS199701/56), 44.177–44.198°S, 147.005–146.96°E, depth 690–1100 m, 29th Jan 1997; **TMAG K4159**, Hill 38 seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor*, stn. 59 (SS199701/59), 44.225–44.19°S, 147.378–146.287°E, depth 1016–1514 m, 30th Jan 1997; **TMAG K4162**, Hill 38 seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor*, stn. 58 (SS199701/58), 44.223–44.187°S, 147.375–146.302°E, depth 1167–1617 m, 30th Jan 1997; **TMAG K4163**, Hill A1 Reserve seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor*, stn. 62 (SS199701/62), 44.328–44.322°S, 147.268–146.325°E, depth 1261–2253 m, 30th Jan 1997; **TMAG K4284**, Hill U seamount, Huon CMR, SW Tasman Sea, Australia, CSIRO *RV Southern Surveyor,* stn. 42 (SS199701/42), 44.29–44.337°S, 147.295–147.238°E, depth 1083–1669 m, 27th Jan 1997; **TMAG K4285**, Mackas seamount, west Huon CMR, SW Tasman Sea, Australia, CSIRO

RV Southern Surveyor, stn. 50 (SS199701/50), 44.21–44.1617°S, 147.043–147.045°E, depth 593–1078 m, 29th Jan 1997; **TMAG K4279**, Big Horseshoe, offshore from eastern Victoria, SW Tasman Sea, Australia, CSIRO, RV *Southern Surveyor,* stn. 152 (SS200001/152), 38.337°S, 149.642°E, depth 991–1008 m, 17th April 2000; **TMAG K4282**, A1 seamount, west of Huon CMR, SW Tasman Sea, Australia, ROV JASON deployed from the U.S. RV *Thomas T. Thompson,* stn 382 (J2-382-015-006), 44.331°S, 146.887°E, depth 1335 m, team led by Dr Jess Adkins & Dr Ron Thresher, 16th December 2008; **TMAG K4283**, seamount west of St. Helens, Tasmania, SW Tasman Sea, Australia, ROV JASON deployed from the U.S. RV *Thomas T. Thompson,* stn 389 (J2-389-009-003), 41.240°S, 148.823°E, depth 1266 m, team led by Dr Jess Adkins & Dr Ron Thresher, 31st December 2008; **MV F173630**, Freycinet Peninsula, 39km NE of Cape Tourville, Tasmania, Australia, *RV Franklin*, stn. SLOPE 84, 41.892–41.889°S, 148.651–148.647°E, depth 732–626 m, 30th Oct 1988; **MV F173638**, Freycinet Peninsula, 54km ENE of Cape Tourville, Tasmania, Australia, *RV Franklin,* stn. SLOPE 82, 41.955–41.898°S, 148.976-148.950°E, depth 1770–1735 m, 30th Oct 1988; **NTM CO12684**, Big Horseshoe, offshore from eastern Victoria, SW Tasman Sea, Australia, CSIRO, RV *Southern Surveyor,* stn. 152 (SS200001/152), 38.337°S, 149.642°E, depth 991–1008 m, 17th April 2000.

Other material:

AM G.13236 (part), off Maria Island, Tasmania, Australia, Australian Antarctic Expedition, 42.6°S, 148.1°E, depth 118–2377 m, 13th Dec 1912 (many fragments and dislodged polyps, probably from two different species).

Description:

Colony form:

The holotype is a bottlebrush-shaped colony with a short, main stem which is missing the holdfast (Fig. 3.67A). It is 120 mm tall and 60 mm broad at the widest point although one large lateral branch has been broken meaning the colony was originally wider. The robust stem is 2.5 mm thick at the base and approximately 34mm tall, at which point it dissipates into a number of branches. There are a few examples of anastomoses. There are no branches on the two proximal internodes of the stem but otherwise there are between 6–8 branches per internode. Primary branches emanate at approximately 45° from all sides of the stem, although there is a tendency for branches to be more crowded and longer on two sides, making the colony slightly laterally compressed. The primary branches are relatively long at 55–85 mm and most reach to the extremities of the colony, although most tips are broken. From them emanate 0–4 secondary branches per internode, also at 45°, with a length of approximately 25 mm (Fig. 3.67B). These are 0.47 mm thick proximally, tapering to fine twigs distally. There are numerous examples of third degree branching, all of which are very fine, delicate twigs, approximately 0.1–0.3 mm thick.

Internodes without coenenchyme are grey to silver, nodes are golden brown and the larger nodes have a dark brown central transverse stripe (Fig. 3.68A). The ends of the nodes are slightly iridescent to silver and the polyps and coenenchyme are light cream.

Polyps:

On the branches, polyps are relatively large, well-spaced and are arranged loosely alternate (Fig. 3.67C, D). They are clavate and tightly curved upwards, with many polyp heads lying against the branch although most commonly the polyps do not touch the surface. There are few polyps on the stem, with most internodes having none or one polyp, although one internode has 3 polyps. On the primary branches there are 0–2 polyps per internode and on the secondary branches 2–4 polyps per internode, seldom up to 6 per internode. They are never crowded with at least 1–1.5 mm between them. The bases of the polyps are quite large at approximately 0.75–0.9 mm (probably due to the regular presence of 2–3 eggs per polyp), the necks are narrower at 0.35–0.5 mm wide and the polyps broaden again at the head to approximately 0.5–0.7 mm wide. Abaxially, polyps are 0.75–1.5 mm long with numerous irregular series of transversely arranged sclerites (Fig. 3.67C–E). The sclerites tend to be slightly more crowded on the adaxial side. There are few juvenile polyps and no modified brooding polyps. The tentacles are usually folded into or bunched above the mouth of the polyp forming a rounded or pyramidal summit (Fig. 3.67C–E).

Axis:

Internodes are circular in cross-section at the proximal ends of the branches and stem with many low, indistinct primary ridges which usually run longitudinally but can slightly twist around the internode (Fig. 3.68Aa). The widest internodes on the stem are 2.5 mm thick and have up to 40 low primary ridges. On the primary branches a proximal internode is 1.5 mm thick with approximately 20 low primary ridges. Distally, the number of ridges decreases (Fig. 3.68B) and eventually the internodes are square in cross-section with four corner ridges. A number of the proximal internodes of the primary branches are swollen such that they are considerably wider than the second internode (Fig. 3.68C). They are 1.5 mm thick proximally, tapering to 0.7–0.9 mm at the next internode and eventually to a fine point distally. The stem has a few short proximal internodes (1–1.5 mm long), but otherwise internodes of the stem are 2.5–4.2 mm long and nodes are 0.8–1.1 mm long. On the branches, internodes are between 4.25–5.5 mm long with nodes 0.3–0.6 mm long. There is a tendency for some of the distal internodes to have some slight curves and bends.

Sclerites:

A thin, single layer of sclerites cover the polyps and colony surface. The polyp body has scales arranged transversely in 16–20 irregular series, each sclerite slightly overlapping the one above (Fig. 3.67C–E). The anthopoma has complex octants consisting of 6–8 small sclerites, arranged obliquely to longitudinally, and interlocking together to form a protective layer (Fig. 3.68D–F). Many of the anthopomal sclerites are robust, narrow, tuberculate rods with ends developed into spikes and thorns (Fig. 3.69A). They tend to be aligned longitudinally in the octants, especially in the distal parts and on the outer margins of the array. Other anthopomal sclerites are irregularly shaped often with broadened ends (Fig. 3.69Aa). These are usually arranged at the base of the octant forming the widest part (Fig. 3.68F). There are also a few flattened scales with minimal tubercles and spines (Fig. 3.69Ab) which are probably from the transition point between the anthopomal and tentacle sclerites. Most anthopomal sclerites are from 0.13–0.26 mm long.

The tentacles have a single row of crescentic scales arranged transversely (Fig. 3.69B) and about 0.07–0.14 mm long. Most have irregularly dentate margins, although some have rounded tubercles on their distal margin. There are very few tubercles on the surface of the sclerites.

The polyp body sclerites are broad, often very irregular, thick, tuberculate scales, particularly large at the top of the polyp, grading to smaller sclerites towards the base (Fig. 3.70). Many of the larger, irregular sclerites have complex spines and tubercles around the margin, large complex tubercles on the surface and are thicker than is common in other *Primnoisis* species (Fig. 3.70a). Proximal sclerites are shorter with simple tubercles. There are few pronounced marginal spines and little curvature in the sclerites making their original orientation on the polyp sometimes difficult to discern, although root-like processes on some sclerites can indicate the proximal margin (Fig. 3.70b). There is a continuum of sclerite length from approximately 0.2–0.36 mm and width from 0.07–0.185 mm with an average width to length ratio of 0.44. There are some irregularly triangular sclerites (Fig. 3.70c) which sit at the junction between the polyp body sclerites and the anthopoma.

Coenenchyme sclerites are moderately tuberculate, slightly flattened rods (Fig. 3.71) which are arranged in a single layer longitudinally to obliquely along the branches (Fig. 3.68D) and are 0.067–0.18 mm long. Some are not flattened with relatively large tubercles.

Variability:

Colonies resemble the holotype growth form with a broadly bottlebrush-structure, many lateral branches and crowded twigs. Recently collected colonies had pink to dark cream polyps before preservation (Fig. 3.72A, B) and preserved colonies are usually white to dark cream (Fig. 3.72C). The nodes are often iridescent (Fig. 3.73A) or can be light pink to yellow, usually making them obvious in the crowded branches. Like the holotype, most colonies are quite robust, with a relatively thick stem and primary branches but the twigs are fragile and easily broken. One small colony collected from the east coast of Tasmania, has only sparse branching with very fine, fragile branches (Fig. 3.74A). Holdfasts when present are usually small, hard, roughly circular extensions of the basal calcareous internode (Fig. 3.72C).

In the paratype colonies, polyps resemble those in the holotype; that is, they are arranged loosely alternate, are tightly curved distally and they do not become more crowded at the branch tips (Figs. 3.72D, E; 3.73A, B; 3.74B). Most are around 1 mm long and juvenile polyps seem rare.

There is some variation of sclerites from the paratypes when compared with those from the holotype. For example, the robust, straight-sided rods which are common in the anthopomas of the holotype (Fig. 3.69A) are often not the dominant sclerite type in the anthopomas of the paratypes. In samples TMAG K4278 and TMAG K4283 the anthopomal sclerites are shorter, often wider and more irregular those in the holotype (Figs. 3.73C; 3.74C). Tuberculate anthopomal rods are present in colony NTM CO12684 but are not common (Fig. 3.72Fa). Tentacle sclerites (Figs. 3.72G; 3.73D; 3.74D) and coenenchymal sclerites (Fig. 3.74F) do not differ significantly from the holotype. In some of the paratypes the polyp body sclerites have more pronounced, regular marginal spines, especially on the distal margin (Fig. 3.73Ea), tend to have greater curvature and although the large irregular sclerites are present (Fig. 3.73Eb) they are less common than in the holotype. Sample NTM CO12684, with the largest geographic separation from the holotype, resembles it by having large, irregularly shaped polyp body sclerites with minimal regular marginal spines but differs somewhat by having generally smaller sclerites and a more substantial coverage of tubercles on almost all sclerites (Fig. 3.72F–H). Colony TMAG K4283 also has smaller polyp body scales, which are more regular than those of the holotype. Some have rounded marginal spines and tubercles and all are without any root-like processes (Fig. 3.74E).

All of these colonies were collected from the southern Tasmanian seamounts, off the east coast of Tasmania and from the south east coast of Victoria with the majority found at depths below 800 m. There are no consistent morphological variations concordant with distribution or depth differences amongst these samples.

Distribution:

South and east of Tasmania, south east Victoria, Australia.

Depth:

593–2253 metres.

Remarks:

This species represents another extension of the genus *Primnoisis* into temperate waters, and is mirrored by the record of *Primnoisis rigida* at a similar latitude in the Atlantic Ocean. Some samples were collected in deep waters off the Australian mainland continental shelf and may extend further north and west at these depths.

The morphology of the species places it indisputably in *Primnoisis*, with a fine, bottlebrush-shaped growth form, internodes without detailed ornamentation, small polyps covered in transversely arranged scales and an anthopoma consisting of a complex of small sclerites, arranged obliquely and longitudinally. In particular, this species is very similar to other species in the new subgenus *Delicatisis* (*P. rigida, P. delicatula*, *P. formosa, P. gracilis, P. millerae* n. sp. and *P. niwa* n. sp). However, molecular results show a surprisingly large divergence of this species from some of these morphologically similar species (see section 3.3.3). Geographic isolation is the obvious point of difference with *P. tasmani* n. sp. only found on the continental shelf around Tasmania and the south east region of mainland Australia while the other similar species appear to be restricted to the Antarctic continent (*P. delicatula, P. formosa, P. gracilis, P. millerae* n. sp.) or Macquarie Ridge (*P. niwa* n. sp.). *P. rigida* was found in deep temperate waters like *P. tasmani* but no recently collected material was available for molecular analysis. *P. tasmani* n. sp. appears to have been isolated from congeners, which have developed many genetic differences but have not resulted in large morphological differences. This raises interesting questions or possibilities such as overlooked morphological features which may reflect this phylogenetic difference. The species remains unplaced to subgenus due to the conflict between morphological similarity with *P.* (*Delicatisis*) but a closer genetic relationship to *P.* (*Primnoisis*).

Using morphological differences in isolation to delimit this species from those in the *P. (Delicatisis)* subgenus is difficult, although the large, thick and complex polyp body sclerites appear specific to this species. Large, robust tuberculate rods, common in the anthopoma, differentiate *P. tasmani* n. sp. from *P. delicatula* as does colony form and size of the polyp body sclerites*.* *P. formosa* and *P. niwa* n. sp. have similar bottlebrush colony forms to *P. tasmani* n. sp.*,* similar sized polyps and some similarity in anthopomal sclerites but both species have narrower body sclerites with more regular edge spines than *P. tasmani* n. sp. Similarly, *P. millerae* n. sp. is distinguished from *P. tasmani* by having polyp body sclerites with regular, simple tubercles and a finely branched, crowded colony form. *P. gracilis* has similar polyps to *P. tasmani* n. sp. but they are very crowded and have flat body sclerites with few tubercles and flattened and jagged marginal spines.

P. antarctica, P. fragilis, P. erymnos n. sp. and *P. chatham* n. sp.*,* from the *P. (Primnoisis)* subgenus, all have large, mostly perpendicular polyps with large, flat scales and robust, rigid colonies.

Etymology:

The species name derives from two sources—after my wonderful son, Tasman, and also from the locality of the majority of the specimens, an area which is known colloquially as the Tasmanian seamounts.

3.3.3 Genetic relationships among morphospecies of *Primnoisis*

3.3.3.1 Sequencing success and alignment

A total of 55 *Primnoisis* sequences were obtained for the mtMutS region and 53 for the igr1-COI region (Table 3.4) from those specimens used in the morphological study which were thought to be likely candidates for successful sequencing. Despite multiple attempts and the use of internal primers, some specimens could not be amplified successfully and/or good quality sequences could not be obtained despite the fact that they were from recent collections. In addition, for some individuals sequence data from only one of the two gene regions was obtained. Suboptimal sequences were discarded.

For mtMutS, sequences varied from 551 to 918 bp long (Table 3.4) with all but one sequence longer than 740 bp. For this short sequence, only mtMutSA could be successfully sequenced with the internal primer. The longer sequences included the ND4 region upstream of mtMutS (obtained when using the ND42475F primer) but analyses were conducted on trimmed sequences without the ND4 region. Alignment was unambiguous with no insertions or deletions. Once the sequences were aligned, the sequences were trimmed to 805 bp, with some sequences missing end portions of the full length. These sequences revealed 43 variable sites, with 36 of those parsimony informative.

For igr1–COI, sequences varied from 551 to 1052 bp long (Table 3.4). There were three specimens where only igr1–COIB was able to be sequenced with the internal primers and these were removed, but the single specimen with only igr1–COIA sequenced was retained as it included the more variable (and therefore more phylogenetically useful) igr1 region. All other sequences were longer than 873 bp. Alignment was unambiguous although the igr1 region showed significant variation with an inconsistent INDEL at site #71 and a 10 bp INDEL at site #116 for *P. (Primnoisis)* specimens, a microsatellite of repeating TA which varied from 2–8 nucleotides long at site #98 for *P. (Delicatisis)* specimens, and a deletion at site #87 for all *P. tasmani* n. sp. specimens. After alignment, trimming and coding of the INDELS, the final alignment of 867 nucleotide positions had 28 variable positions with 25 of those parsimony informative.

Table 3.4. Taxa for which sequences of mtMutS and igr1–COI were obtained, the number of specimens where amplification was attempted and the number and length of sequences obtained.

Taxa	Attempted	mtMutS		igr1–COI		mtMutS-igr1–COI
		Sequenced	Length (bp)	Sequenced	Length (bp)	Sequenced
P. fragilis	24	21	751–912	22	551–998	20
P. chatham n. sp.	5	3	791–826	3	927–979	3
P. erymnos n. sp.	4	2	551–826	2	973–1048	2
P. gracilis	9	5	759–900	6	873–993	5
P. delicatula	2	2	791–815	2	961–1007	2
P. formosa	10	7	744–904	7	948–1008	7
P. niwa n. sp.	12	4	760–826	4	970–1017	4
P. millerae n. sp.	5	3	764–810	2	1007	2
P. tasmani n. sp.	16	8	743–918	5	963–1053	5

3.3.3.2 Phylogenetic analyses as support for morphological decisions

The mtMutS gene region alone and the gene regions concatenated generated concordant phylogenetic trees with both Bayesian and maximum likelihood approaches (Figs. 3.75, 3.76). Only Bayesian analysis is included for the concatenated gene regions as the data required partitioning into two different models and the ML analysis software used cannot run partitioned models. Trees generated using the igr1–COI gene region only failed to distinguish some clades and produced slightly different relationships at a generic level (Fig. 3.77). The Mopseinae genera, *Chathamisis* and *Echinisis*, formed an effective outgroup in the mtMutS tree, clearly distinct from *Primnoisis.* However, sequences of the igr1–COI gene region were not available for these genera. The outgroups used initially for the igr-CO1 analysis (*Notisis* spp and an undescribed genus) were found to be very closely related to *Primnoisis* species, falling among the *Primnoisis* specimens, and thus were ineffective as outgroups. *Notisis* has complex anthopomas similar to *Primnoisis* but has spines on the axis which *Primnoisis* lacks. Alderslade (1998) considered this a major morphological trait, separating large groups of Mopseinae genera. Similarly the undescribed genus has quite different sclerites to those from the *Primnoisis* specimens and is easily separated morphologically. The phylogenetic position of these genera raises questions about the monophyly of the genus *Primnoisis*. In order to focus solely on specimens that were morphologically determined as *Primnoisis* and assess their relative relationships, for the final concatenated analysis and for the igr1–COI only analysis, sequences from *Keratoisis sp* were used as an outgroup.

Primnoisis specimens divided into three genetic groups which were consistent both in Bayesian and ML analysis and when using the gene regions concatenated or alone (Figs. 3.75–3.77). Two of these genetic groups correspond to morphological groupings and have been recognised here as the new subgenera—*P. (Primnoisis)* and *P. (Delicatisis)* (section 3.3.2). The third group, consisting of the clade of *P. tasmani* n. sp. specimens, is significantly distant from and basal to the other *Primnoisis* specimens and suggests an historical divergence which could be expected to be reflected in morphology. There is also geographic separation of this group of specimens, all being from waters around Tasmania. However, morphologically *P. tasmani* is surprisingly similar to species in *P. (Delicatisis)*. The relatively high level of genetic difference between *P. tasmani* and species within *P. (Delicatisis)* suggests there may be unrecognised, non-traditional morphological characteristics within this clade which could be phylogenetically informative.

There is a possibility that the three groups identified within *Primnoisis* specimens could be unrecognised genera, especially considering the unresolved relationships with *Notisis* and the undescribed Mopseinae genus, but very few sequences of these two genera were available thus the validity of their placement dividing the *Primnoisis* specimens remains unconfirmed. Along with the *P. tasmani* n.sp. sequences, they were placed on an indefinite five-way node in the trees generated from igr1–COI gene region alone, and only once INDELS were coded. This indicates the INDELS and microsatellite in the igr1 region appear to be phylogenetically informative at a generic or sub-generic level but how this information is included in the analyses may be significant (Saurabh et al. 2012). Finally, genetic distances between the other Mopseinae genera *Echinisis/ Chathamisis* and *Primnoisis* (both subgenera together) are considerably greater than those between the three *Primnoisis* genetic groups (Table 3.5 and see below).

At this stage, there is insufficient justification for constructing new genera for these groups within *Primnoisis* as the morphological differences do not compare with others used to differentiate Mopseinae genera (for examples see Alderslade 1998). Furthermore, the anomalous phylogenetic position of *Notisis* and the undescribed genus within *Primnoisis* samples is based on few specimens, and genetic distances between the subgenera fall within the (admittedly large) range found for other octocoral congeners (Baco & Cairns 2012; Herrera et al. 2012; McFadden et al. 2011; Pante & France 2010) and are much less than between other genera in the subfamily Mopseinae. However, the designation of *Primnoisis* as a monophyletic genus is also impossible at this stage and further work is needed, particularly future molecular research on *Notisis* and the undescribed genus, and further morphological research on *P. tasmani* n. sp, to fully resolve this genus.

Clades within the three genetic groups of *Primnoisis*

Within each of the three genetic groups, clades were generally consistent between trees generated with the concatenated gene regions and those generated using mtMutS gene region only (Figs. 3.75; 3.76). Despite the igr1 region having significant variation and numerous INDELS, those differences were only informative at the sub-genus level, with both igr1 and COI being almost invariant within the three genetic groups, thus failing to distinguish species (Fig. 3.77 and Table 3.7).

The distances and variability amongst some sequences are very low (see below) and are reflected in the poor support and resolution of the minor clades. Nevertheless, in some cases the clades provided independent support for morphological species decisions and acted as a trigger for re-examination of specimens for morphological differences (see section 3.3.2).

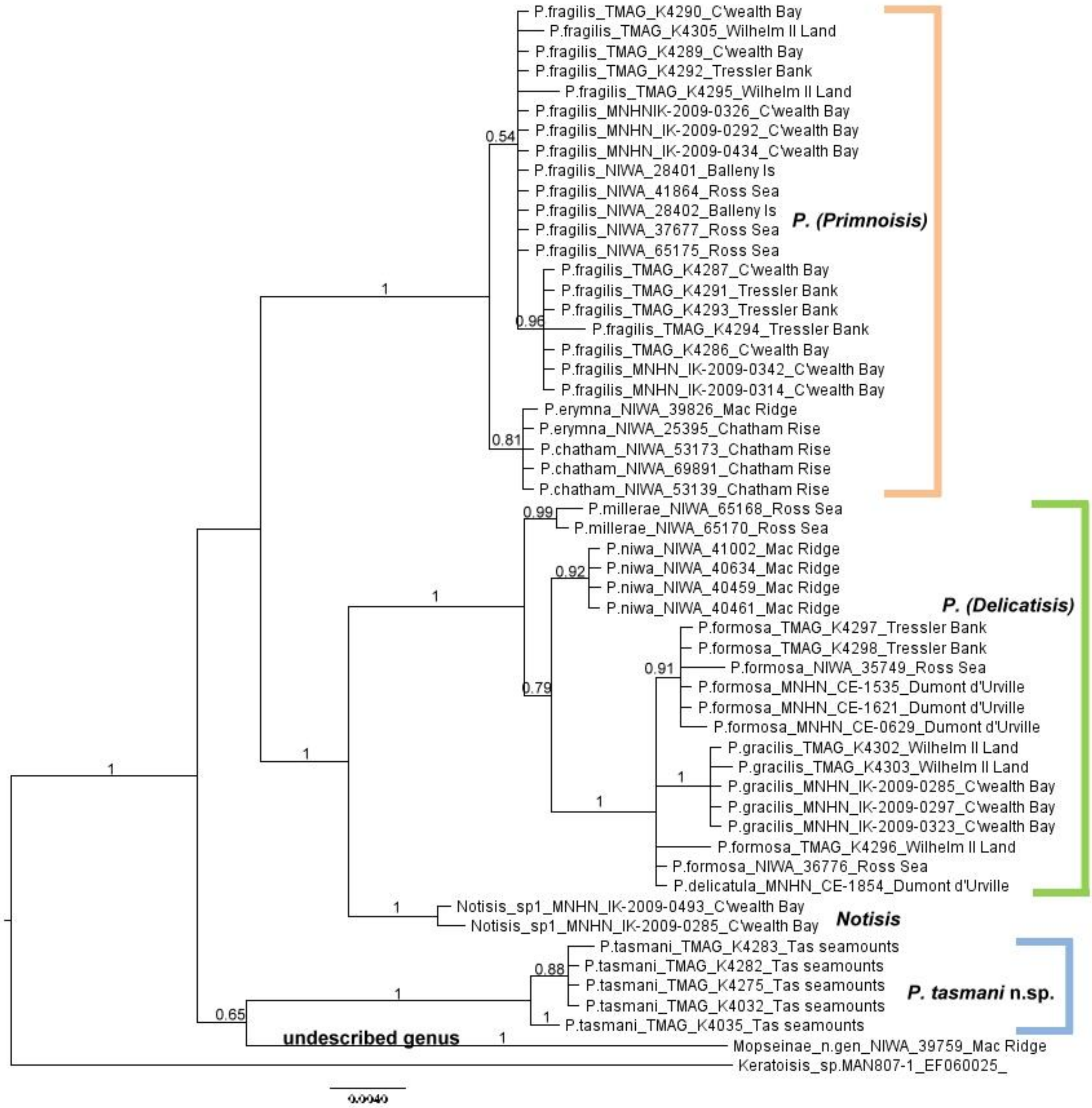


Figure 3.75. Bayesian 50% majority rule consensus tree generated from nucleotide sequences for the mitochondrial gene regions mtMutS and igr1–COI concatenated. Numbers shown are posterior probabilities (partitioned model, 8000000 generations, burnin=20000, split freq=0.002, PSRF 1.000-1.001).

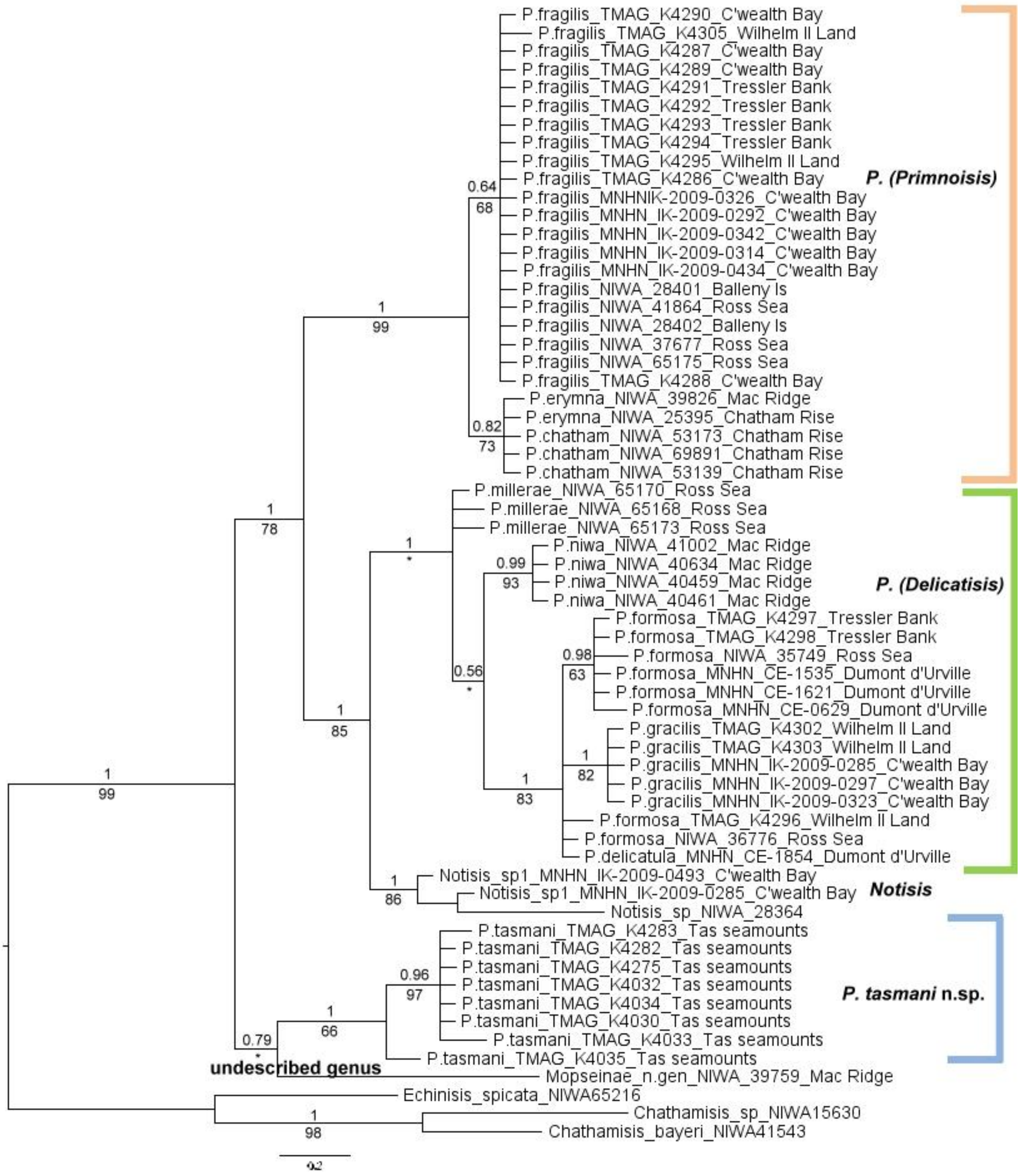


Figure 3.76. Bayesian 50% majority rule consensus tree generated from nucleotide sequences for the mitochondrial gene region mtMutS (GTR+G model; 7000000 generations, burnin=17500, split freq =0.002, PSRF 1.000–1.004) Bayesian posterior probabilities for each node shown above the node, ML bootstrap support as a percentage of 500 bootstrap replicates below the node. * indicates branch difference from the ML analysis.

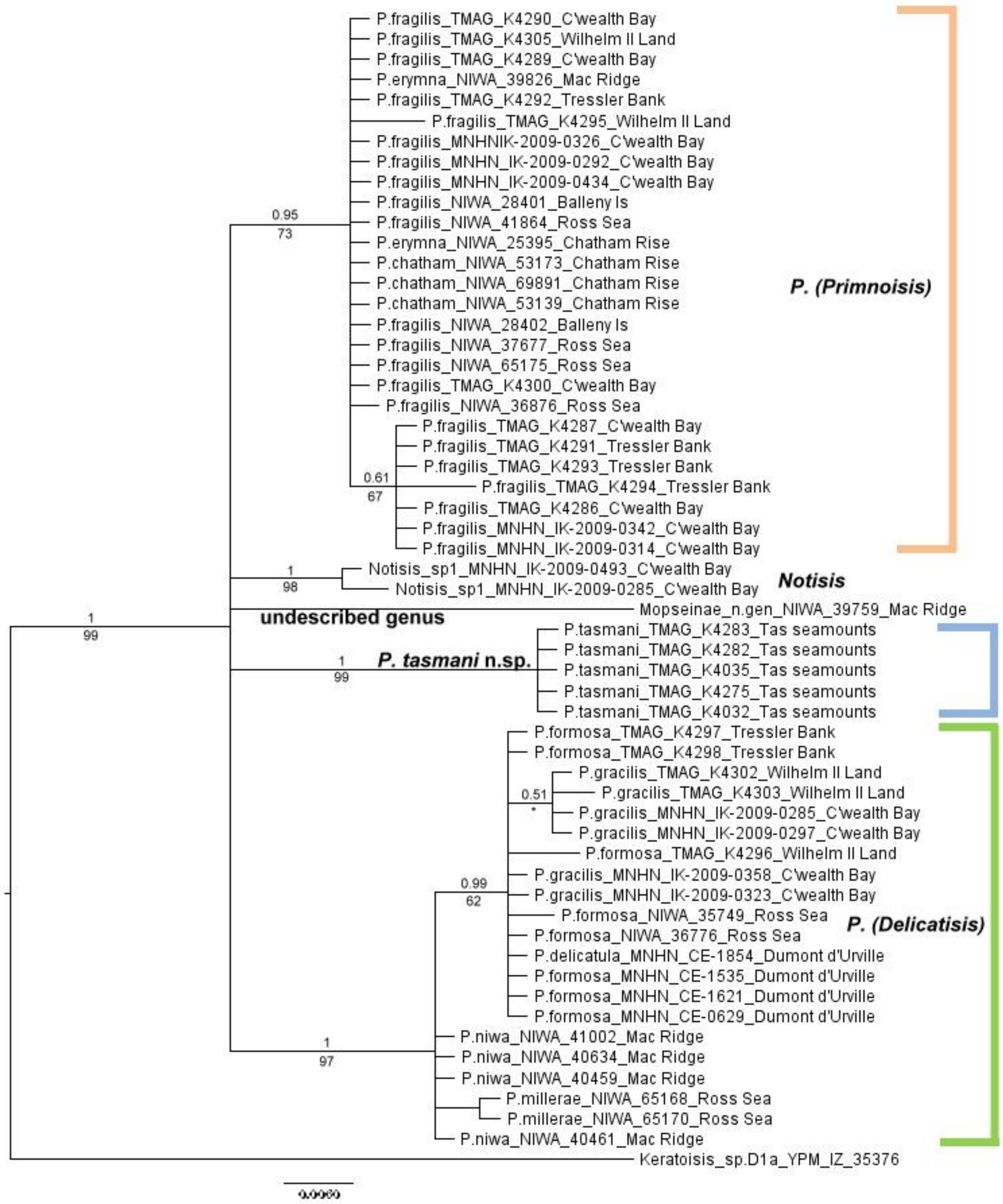


Figure 3.77. Bayesian 50% majority rule consensus tree generated from nucleotide sequences for the mitochondrial gene regions igr1–COI (GTR+I model; 6000000 generations, burnin=15000, split freq =0.002, PSRF 1.000-1.004). Bayesian posterior probabilities for each node shown above the node, ML bootstrap support as a percentage of 500 bootstrap replicates below the node. * indicates branch difference from the ML analysis.

3.3.3.3 Genetic distances as support for morphospecies

Genetic distance estimates of *Primnoisis* from other Mopseinae genera were possible based on the mtMutS region (Table 3.5). For the igr1–COI region, only the sequences generated in this study for

Notisis sp. and the undescribed Mopseinae genus were available and because their relationship with *Primnoisis* is unresolved, genetic distances based on COI were not examined here.

Echinisis, Chathamisis and the undescribed genus specimens were clearly separated from *Primnoisis* (all three genetic groups included) with pairwise p-distances of 0.043, 0.050 and 0.038 (3.9%, 5.0 % and 3.8%) respectively (Table 3.5). *Notisis* was genetically closer to *Primnoisis* despite being morphologically distinct (pairwise p-distances of 0.016) (Table 3.5). In fact, *Notisis* was more closely related to the subgenera *P. (Delicatisis)* specimens (0.015) and *P. (Primnoisis)* specimens (0.016) than the subgenera were to each other (0.022). *P. tasmani* n.sp. specimens were closer genetically to the *P. (Primnoisis)* group (0.016) than the *P. (Delicatisis)* group (0.026) despite being morphologically much more similar to the latter, one of the reasons this species remains unplaced to subgenus. Baco & Cairns (2012) found comparable intergeneric p-distances of 0.35–3.52% (0.0035–0.0352) between genera within Primnoidae, although the range is very large.

An average intrageneric p-distance of 0.014 for all *Primnoisis* specimens is within the range of intrageneric p-distances found for other Calcaxonians by McFadden (2011), using the mtMutS gene region only (0–1.96% (0–0.0196)). *Primnoisis* is distinct from some sister genera with genetic distances and internal diversity within the genus inside the expected ranges but the relationship with *Notisis* in particular is unresolved.

Within the genus *Primnoisis*, interspecific p-distances varied from 0.00–0.026 using the mtMutS gene region (Table 3.5). The same three groups within the genus emerge as in the phylogenetic trees (*P. (Primnoisis)* – orange, *P. (Delicatisis)* – green, *P. tasmani* n. sp. – blue in Table 3.5). Within each of these groups mean interspecific p-distances are low (0.003–0.015) reflecting sequence differences of only a few nucleotides in most cases. However, most of these morphospecies are genetically discernible using mean interspecific genetic distance if a threshold value of >0.3% is adopted as suggested for *Alcyonium* species in McFadden et al. (2014).

Intraspecific genetic distances were all very low with a maximum p-distance of 0.002 or three nucleotide differences (Table 3.5).

Table 3.5. Mean genetic distances for *Primnoisis* mtMutS sequences included in phylogenetic analysis.

Intergeneric p-distances (sub-generic)		**1**	**2**	**3**	**4**	**5**	**6**	***Primnoisis* (all species)**
	1. P. (Primnoisis)							-
	2. P. (Delicatisis)	0.022						-
	3. Notisis	0.016	0.015					0.016
	4. **Undescribed genus**	0.037	0.042	0.037				0.038
	5. Chathamisis	0.050	0.051	0.050	0.060			0.050
	6. Echinisis	0.040	0.049	0.037	0.055	0.051		0.043
	7. P. tasmani **n.sp.**	0.016	0.026	0.016	0.032	0.045	0.035	-
Interspecific p-distances		**1**	**2**	**3**	**4**	**5**	**6**	**7**
Primnoisis (Primnoisis)	**1. *P. fragilis***							
	2. *P. chatham* n. sp.	0.003						
	3. *P. erymna* n. sp.	0.003	0.000					
Primnoisis (Delicatisis)	**4. *P. gracilis***	0.017	0.015	0.015				
	5. *P. formosa*	0.022	0.019	0.019	0.004			
	6. *P. niwa* n. sp.	0.026	0.023	0.023	0.015	0.013		
	7. *P. millerae* n. sp.	0.023	0.020	0.020	0.012	0.010	0.003	
Primnoisis tasmani n. sp.	**8. *P. tasmani* n. sp.**	0.016	0.013	0.013	0.022	0.026	0.025	0.023
Intraspecific p-distances (# bp differences)	0.000–0.002 (0–3)							

3.3.3.4 Character-based analysis and morphology combined for species delineation

When combined and used in a character-based analysis, the gene regions employed in this study appear to have sufficient variation for delineation of some species. Character-based analysis is a useful technique for comparing closely related taxa and gene regions with low levels of variability and in some cases has been shown to be more effective for octocorals than distance-based analyses (Baco & Cairns 2012; McFadden et al. 2011).

Within the new subgenus Primnoisis (*Primnoisis*)

In the *P. (Primnoisis)* group, sequences of all individuals were identical with the exception of two base pairs in the mtMutS gene region (Table 3.6; positions #252 and #292). These are the only nucleotide differences across both gene regions among the three species (*P. fragilis, P. chatham* n. sp. and *P. erymna* n. sp.) sequenced in the subgenus. These species are distinguished on morphological and geographical differences but genetic variation does not consistently reflect these differences. In fact the morphological and geographic differences among the specimens in the large *P. fragilis* clade are substantial (see section 3.3.2) yet the specimens have almost identical sequences. Two haplotypes were found within the *P. fragilis* clade, with a single INDEL at position #71 (Table 3.7) in the igr1 gene region for seven specimens. There is a large morphological range within *P. fragilis* specimens and future work may be able to elucidate these differences, but with no consistent morphological or geographical characters distinguishing these seven specimens from the other *P. fragilis* specimens this SNP is interpreted as intraspecific variation or sequencing error.

P. fragilis specimens, which only occur on the Antarctic continent and have polyp body sclerites which are large, tuberculate, toothed scales, are separated from *P. chatham* n. sp. and *P. erymna* n. sp. in a poorly supported clade in the phylogenetic trees (Figs. 3.75–3.77), reflective of the two nucleotide differences among them. *P. chatham* n. sp. specimens are all from the temperate Chatham Rise seamounts on the east coast of New Zealand, and have small, flattened, serrated scales for the polyp body sclerites while *P. erymna* n. sp. specimens are all from the subantarctic Macquarie Ridge (except a single *P. erymna* n. sp. specimen from Chatham Rise) and have robust, rounded, tuberculate spindles for the polyp body sclerites. These latter two species share a haplotype; however, considering *P. erymna* n. sp. is only represented by two sequences and *P. chatham* by three, conclusions on genetic differences are necessarily weak. Nevertheless, considering the morphological and geographical distinctions among these species, these gene regions do not seem to be very variable within this subgenus. There is also the species *P. antarctica* in the subgenus but unfortunately no specimens sequenced successfully in this project.

Table 3.6. Single nucleotide differences between mtMutS haplotypes within *Primnoisis.*

Morphospecies	n	mtMutS																																		
		101	**119**	**130**	**139**	**143**	**184**	**220**	**223**	**225**	**233**	**335**	**252**	**266**	**268**	**287**	**292**	**389**	**392**	**422**	**443**	**467**	**568**	**575**	**584**	**587**	**648**	**686**	**687**	**729**	**733**	**739**	**753**	**754**	**766**	**818**
P. fragilis	21	T	A	T	G	A	C	T	T	C	A	G	G	G	T	A	T	A	T	T	A	G	A	A	T	T	T	A	A	T	G	A	A	T	T	A
P. chatham n. sp.	3	T	A	T	G	A	C	T	T	C	A	G	A	G	T	A	G	A	T	T	A	G	A	A	T	T	T	A	A	T	G	A	A	T	T	A
P. erymna n. sp.	2	T	A	T	G	A	C	T	T	C	A	G	A	G	T	A	G	A	T	T	A	G	A	A	T	T	T	A	A	T	G	A	A	T	T	A
P. gracilis	5	G	A	T	A	G	C	C	T	C	C	A	A	G	T	G	T	G	T	T	A	A	A	C	T	C	A	C	G	C	G	C	G	T	T	A
P. delicatula	2	G	A	T	A	G	C	C	T	C	C	A	A	G	T	G	T	G	T	T	A	G	A	C	T	C	A	C	G	C	G	C	G	T	T	A
P. formosa	7	G	A	T	A	G	A	C	T	C	C	A	A	G	T	G	T	G	T	T	A	G	A	C	T	C	A	C	G	C	G	C	G	T	T	A
P. niwa n. sp.	4	A	A	T	A	G	C	C	T	T	A	A	A	G	G	G	T	G	G	C	A	G	A	A	T	C	A	C	G	C	G	C	G	T	T	A
P. millerae n. sp.	3	A	A	T	A	G	C	C	T	T	A	A	A	G	G	G	T	G	G	T	A	G	A	C	T	C	T	C	G	C	G	C	G	T	T	A
P. tasmani n. sp.	8	G	G	C	G	G	C	T	G	T	A	A	A	A	T	A	T	A	T	T	G	G	C	C	C	C	C	C	G	C	T	A	G	G	C	G

Within the new subgenus Primnoisis (Delicatisis)

Closely related species groups examined at a character level include *P. gracilis* and *P. formosa* which have very similar sequences. These species, each with more than one haplotype, are separated by 2–3 nucleotide difference within mtMutS, (Table 3.6; positions #184, #392and #467) and 2–8 nucleotides in the igr1 region depending on the length of a small microsatellite (Table 3.7; positions #98–105). In the phylogenetic trees both species are usually positioned on poorly supported clades (Figs. 3.75–3.77). The two species are sympatric, with multiple specimens of each species collected at three Antarctic continental sites. However, there are consistent and predictable morphological differences between the two groups (section 3.3.2) and combined with the molecular differences they have been retained as separate species. A small group of specimens have individual nucleotide differences which mean the specimens are positioned inconsistently. One of the three specimens differs from the dominant haplotype by one nucleotide (Table 3.6; position #184) and is distinguishable morphologically as *P. delicatula* (section 3.3.2). The two remaining specimens differ at two other bases but are indistinguishable based on morphology and geography from the *P. formosa* specimens. These SNPs may simply represent sequencing error and highlight the difficulty inherent in using only a small number of SNPs in isolation for species delineation especially with small sample sizes.

Table 3.7. Single nucleotide differences between igr1 haplotypes within *Primnoisis.*

		igr1																							
Morphospecies	**n**	**71**	**87**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**	**101**	**102**	**103**	**104**	**105**	**181**	**182**	**183**	**184**	**185**	**186**	**187**	**188**	**189**	**190**
P. fragilis H1	15	G	A	G	G	T	A	T	-	-	-	-	-	-	-	-	A	T	G	T	G	C	A	T	A	G
P. fragilis H2	7	-	A	G	G	T	A	T	-	-	-	-	-	-	-	-	A	T	G	T	G	C	A	T	A	G
P. chatham n. sp.	3	G	A	G	G	T	A	T	-	-	-	-	-	-	-	-	A	T	G	T	G	C	A	T	A	G
P. erymna n. sp.	2	G	A	G	G	T	A	T	-	-	-	-	-	-	-	-	A	T	G	T	G	C	A	T	A	G
P. gracilis H1	1	A	A	T	A	T	A	T	A	T	A	T	A	T	A	T	-	-	-	-	-	-	-	-	-	-
P. gracilis H2	5	A	A	T	A	T	A	T	A	T	A	T			-	-	-	-	-	-	-	-	-	-	-	-
P. delicatula	2	A	A	T	A	T	A	T	A	T																
P. formosa	7	A	A	T	A	T	A	T	A	T	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. niwa n. sp.	4	A	A	T	A	T	A	T	A	T	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. millerae n. sp.	2	A	A	T	A	T	A	T	A	T	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. tasmani n. sp.	5	A	-	G	G	T	C	T	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

P. niwa n. sp. and *P millerae* n. sp. are closely related to each other with only three nucleotide differences between them in mtMutS (Table 3.6, positions #422, #575 and #648) and a single nucleotide difference in the COI region (Table 3.8, position #492) with the two species usually weakly supported in separate clades (Figs. 3.75–3.77). *P. niwa* n. sp. is restricted to the subantarctic

Macquarie Ridge site while *P. millerae* n. sp. occurs on the Antarctic continental shelf and there are small but consistent morphological differences (section 3.3.2).

Table 3.8. Single nucleotide differences between COI haplotypes within *Primnoisis.*

		COI															
Morphospecies	**n**	**271**	**291**	**444**	**453**	**474**	**492**	**495**	**510**	**516**	**556**	**571**	**636**	**637**	**693**	**765**	**858**
P. fragilis	22	G	A	T	T	C	G	T	G	T	A	T	G	G	C	A	T
P. chatham n. sp.	3	G	A	T	T	C	G	T	G	T	A	T	G	G	C	A	T
P. erymna n. sp.	2	G	A	T	T	C	G	T	G	T	A	T	G	G	C	A	T
P. gracilis	6	T	C	G	T	C	G	C	A	T	G	T	G	G	T	A	C
P. delicatula	2	T	C	G	T	C	G	C	A	T	G	T	G	G	T	A	C
P. formosa	7	T	C	G	T	C	G	C	A	T	G	T	G	G	T	A	C
P. niwa n. sp.	4	T	C	G	T	C	G	C	G	T	G	T	G	G	T	A	T
P. millerae n. sp.	2	T	C	G	T	C	T	C	G	T	G	T	G	G	T	A	T
P. tasmani n. sp.	5	T	A	T	G	T	G	T	G	C	A	G	T	A	T	G	T

P. tasmani n. sp. specimens form a single well-supported clade except for one specimen (TMAG K4035) which is separated based on two nucleotide differences in mtMutS (Figs. 3.75–3.77). There are no major morphological differences between the specimens and the divergent specimen was collected on the same seamount as another specimen, TMAG K4033. This divergence is considered intraspecific variation only, given the lack of other supporting factors such as morphological or geographical differences. However, sequencing additional specimens may allow further clarification of these SNPs.

P. tasmani is more closely related to the undescribed Mopseinae genus than to the other *Primnoisis* specimens despite morphological evidence to the contrary. The undescribed genus has spiky sclerites with substantially different shapes and is easily separated from *P. tasmani* n. sp. specimens while species within *P. (Delicatisis)* are very similar morphologically to *P. tasmani* n. sp. (see section 3.3.2). This divergence, although not reflected morphologically, is coupled with geographic isolation with the *P. tasmani* n. sp. samples restricted to the Tasmanian coastal shelf while the other *P. (Delicatisis)* samples are found on the Macquarie Ridge and on the Antarctic continent. Geographic separation may have isolated *P. tasmani* n. sp. from evolutionary pressures affecting the morphology of other species or there may be undetected morphological differences in non-traditional taxonomic characteristics.

3.4 Discussion

3.4.1 Phylogeny of *Primnoisis*

Primnoisis was found to be a valid genus within the subfamily Mopseinae and is consistent with the genus definition in general use (Alderslade 1998; Bayer & Stefani 1987b). Alderslade (1998) revised Mopseinae genera with transversely arranged scale-like sclerites and with planar or close to planar colonial growth forms. During this revision, he briefly assessed *Primnoisis* and, combined with Bayer & Stefani's (1987b) re-description of the type species *P. antarctica,* clearly established the diagnostic characteristics of the genus. Specimens investigated here have supported these characteristics of a complex anthopoma consisting of many smaller sclerites arranged longitudinally to obliquely in the octants; bottlebrush or bushy colony form; scale-like sclerites (mostly) arranged transversely on the polyp body; and internodes without significant ornamentation. Morphologically, these characteristics were found to incorporate specimens that divide into two distinct groups; but these groups are only distinguished by relative or subjective morphological features like size, polyp angle and colony rigidity. These characteristics are not considered comparable to features previously used to delineate genera in this subfamily like the presence and type of spines or cavities in the axis, colony growth form and distinctive anthopomal arrangements (Alderslade 1998; Bayer & Stefani 1987a, 1987b). Molecular results, however, strongly support subdivision within the genus, so in the absence of genus-level morphological distinctions these groups have been designated as new subgenera (*Primnoisis* and *Delicatisis)*.

The molecular results could not clarify all relationships among specimens suspected to be *Primnoisis* or closely related genera. Past molecular research has highlighted the polyphyletic nature of many of the morphologically defined octocoral orders and families and there remain many families that consist of potentially unrelated groups (McFadden et al. 2010). However, genus-level molecular clades that match historical morphological distinctions and existing genus groupings have been found (Benayahu et al. 2012; McFadden et al. 2011; McFadden & van Ofwegen 2012a) although morphological-molecular congruence at a genus level is not always present (McFadden & van Ofwegen 2012c; Wirshing et al. 2005). Levels of variation within the gene regions differ between genera, in some instances with large genetic distances between genera while between others there are low levels of variation, possibly reflecting recent divergence (Sánchez, McFadden, et al. 2003). These conclusions, of course, are dependent on the pre-determined taxonomic groupings expected within a study, i.e. which taxa are presumed to be within or related to any genera based on traditional morphology. Thus there is not always a clear distinction between intra- and inter-generic genetic distances, and determining the monophyly of a genus is potentially confounded by which specimens are included, as few studies include all possible data. Indeed, conclusions by Aguilar-

Hurtado et al. (2012) regarding genera described on traditional morphological features matching molecular clades in the family Melithaeidae were shown to be unsupported in Reijnen et al (2013) who suggest the initial results were a reflection of sampling bias. In this study, it was impossible to confirm *Primnoisis* as a monophyletic genus, foremost due to the position of three specimens morphologically determined as *Notisis.* If these species had not been included in the study then *Primnoisis* would be considered monophyletic, albeit with an indistinct relationship with the single specimen of the undescribed genera. However, the *Notisis* specimens were included precisely because the morphological similarity to *Primnoisis* is such that they were initially mistaken for *Primnoisis* specimens. Based on these molecular results, the morphological definition of *Primnoisis* could be expanded to include these *Notisis* specimens (minor spines sometimes present on the internodes, partly planar colony), and then the genus could be considered monophyletic and with congruence between morphological and molecular results. However, Alderslade (1998) found the presence/absence of spines on the internodes is a fundamental morphological trait and expanding a genus definition to allow both states is potentially problematic for other Mopseinae genera. Further work on *Notisis* specimens, specifically different species to those included here, is necessary to elucidate this relationship.

3.4.2 Congruence of morphological and molecular results for species delineations

Traditional morphological characteristics used to delineate species of *Primnoisis* have been branching forms, polyp distribution and sclerite differences. These are largely subjective and exist along a continuum, hence without the type specimen present for a direct comparison some of the definitions are indistinct and inconclusive. Additionally, two of the type specimens, *P. delicatula* and *P. gracilis,* are probably small fragments of larger colonies so decisions on colony form are problematic. Combining morphological and molecular results here provided an additional independent parameter which, it was hoped, could help highlight phylogenetically informative morphological characteristics. This was successful to a degree with some differences in morphological characteristics (e.g. polyp body sclerites) found to match the lineages mapped using the chosen gene regions. However, these characteristics are still very subjective, for example, *more* crowded polyps or *less* tuberculate sclerites. Thus when DNA sequences are unavailable, which is more often the case than not, the difficulty of morphological overlap remains. Comparing specimens side by side can allow clearer differentiation but assessing species placements in isolation is difficult. Additionally, variability in sclerite shape and ornamentation within a single colony can create confusion. It was hoped that the form and arrangement of the anthopoma combined with the different shapes of the anthopomal sclerites would inform species delineations; however, although general anthopomal sclerite form is used, the anthopoma is similar across species. The arrangement of the sclerites appears to be genera specific, with the general layout of the complex anthopoma relatively consistent.

One interesting pattern found here is the relatively large genetic difference between the *P. tasmani* n. sp. specimens and those specimens from the *P. (Delicatisis)* subgroup. These species are very similar morphologically with tightly curled polyps, small warty sclerites and bushy colonies. However, the *P. tasmani* n. sp. is placed basal to the other *Primnoisis* species and usually grouped with a specimen of the undescribed Mopseinae genus which has very obvious differences in sclerite type and form. There appears to be some factor distinguishing this *Primnoisis* species from the others which is not reflected in the traditional morphological characters assessed. Further work on other characteristics, for example internode or node composition, nematocyst construction or reproductive mode may provide previously overlooked morphological differences which match this molecular distance. Alternatively this population, which was found only on temperate seamounts and continental slopes, may have been isolated from the other morphologically similar *Primnoisis* species which are concentrated on (but not restricted to) the Antarctic continent. Evolutionary pressures specific to the Antarctic continent such as ice scour or local bottle-necks from glacial extension and retraction (Brandt, De Broyer, et al. 2007; Rogers 2007) may have influenced a diversity of genetic adaptations not forced upon *P. tasmani* n. sp. and not reflected in the morphology. This raises the question of how reflective the chosen gene regions are of the traditional morphological characteristics. McFadden & van Ofwegen (2012b) (using the gene regions mtMutS, COI and 28S rDNA) described a cryptic species within the octocoral genus *Incrustatus* which has a genetic distance from its congener greater than any conspecific individual as yet recorded for octocorals, yet the morphological differences are very slight with a microscopic variation in the ornamentation of the coenenchymal sclerites the only detectable difference. In contrast, McFadden & van Ofwegen (2012c), using the same gene regions, established a new genus *Inconstantia*, (sister to *Incrustatus*) which encompasses three species with vastly different morphology but which genetically form a “remarkably homogenous group” with very low genetic distances. Thus, genetic divergence does not always reflect obvious morphological variation and vice versa and, even in closely related genera, the relationship is not consistent.

3.4.3 Effectiveness of the chosen gene regions for species delineation

Within the subgenera, genetic distances between species varied. Clades within *P. (Delicatisis)* differed by a p-distance of 0.003–0.015, were persistent regardless of analysis and matched morphological differences. In contrast, within *P. (Primnoisis)* there were p-distances of 0.000–0.003 among species and only a single persistent division which was based on 2 base pairs. Within one division there are two species (*P. erymna* n. sp. and *P. chatham* n. sp.), distinguished only on morphological differences, which share a haplotype. The comparative difference in genetic variability within the two subgenera may be an artefact of erroneous morphological species boundaries (i.e. arguably *P. erymna* n. sp. and *P. chatham* n. sp. could be considered a single species because they are genetically identical) but equally could represent recent divergence in *P.* (*Primnoisis*) compared with earlier divergence in *P.* (*Delicatisis*). Previous research has found similar examples of large morphological or geographic differences between taxa without the expected genetic differences (Benayahu et al. 2012; Cairns & Baco 2007; McFadden et al. 2011; McFadden & van Ofwegen 2012c) and in most cases the morphological and geographical differences were employed to override the lack of genetic divergence and delineate species regardless. In the case of *P. (Delicatisis)* specimens these gene regions were effective at species delineation and corresponded with geographic and morphological boundaries, but for *P. (Primnoisis)* specimens the gene regions did not always reflect the morphological diversity. Haplotype investigation or character-based analysis of individual SNPs between haplotypes was found to be an effective tool where the genetic variability of gene regions is so low. However, these conclusions based on SNPs were necessarily restricted by having only two gene regions available, both of which are mitochondrial and known to be conserved in octocorals. Additionally, as qualified by McFadden et al. (2011), these haplotype comparisons are most effective in well-studied populations where the significance or persistence of single polypmorphisms can be judged more effectively. Nevertheless, in octocoral phylogenetics, where genetic variability appears to be so low in mitochondrial gene regions and reliable, effective and easily sequenced nuclear gene regions are limited, mitochondrial haplotype comparisons can provide important taxonomic information.

3.4.4 Distribution and endemism

Primnoisis was found to have a southern circumpolar distribution and is confirmed from deep temperate waters as far north as 37°S from the South American continent and 38°S from the Australian continental shelf. Previous inferences that the record of *P. rigida* off Rio de la Plata was perhaps isolated and exceptional (and assumptions that the genus was restricted to Antarctic waters only) have been muted by the abundance of *Primnoisis* specimens collected north of 44°S around Tasmania and on the seamounts of New Zealand. It in fact appears to frequently occur on high latitude southern seamounts and canyons and is particularly common at depths between 100–600 metres on the Antarctic continental shelf.

The specimens collected from north of the Antarctic Circumpolar Front appear to have restricted distributions (see Chapter 4). *P. tasmani* n. sp. is common on the seamounts and the deep continental shelf south and east of Tasmania and was collected from the south east region of the

Australian mainland. *P. niwa* n. sp. is restricted to the Macquarie Ridge, *P. chatham* n. sp. to the New Zealand seamounts and *P. erymna* n. sp. was recorded from both these regions. Those species found on the Antarctic continental shelf have a much more extensive distribution, seeming to extend through at least three sampling points on the continental shelf and probably further around but never north of the circumpolar current. Thus, as the molecular divisions so closely mirrored geographic distribution, location information became extremely important as a starting point for the morphological assessments. The difficulty with restricted populations is assessing their status as true endemic species or local geographic variations influenced by local conditions. Quattrini (2013) found environmental niches such as depth and cold seeps determined species distributions within the Gulf of Mexico and suggests these highly localised environmental variables influence the morphological characteristics used for species delimiting. Miller et al. (2011) found closer relationships with specimens at similar depths at geographically separated sites than those found at different depths on nearby sites, suggesting the question of geographic endemism could perhaps be superseded by environmental endemism. Thoma (2009) found no evidence of endemism in octocoral and antipatharian fauna on the New England and Corner seamounts in the north west Atlantic Ocean and suggests undersampling is the determining factor in restrictive geographic distributions. In this study, there is no suggestion of endemism on individual seamounts (although arguably the molecular markers were insufficiently variable to assess this), but after relatively extensive sampling at most sites, in general species north of the circumpolar front were not found in more than one geographic area. *P. antarctica* specimens were not successfully sequenced here but fresh specimens may counter these geographic patterns as specimens morphologically similar to *P. antarctica* were found on the Isle Kerguelen/Heard Island plateau, distant from the type location. The connectivity between the populations on the Antarctic continent is a striking contrast to those north of the circumpolar front with sympatric populations of *P. gracilis, P. formosa* and *P. fragilis* and with each species collected at more than three geographically separated sites on the continent (see Chapter 4).

3.4.5 Summary

Primnoisis is retained as a valid genus within the family Isididae, and morphological characters previously used to define the genus (Alderslade 1998) are confirmed—bushy or bottlebrush-shaped colonies, complex anthopomas with octants consisting of an array of small, irregular sclerites arranged longitudinally and obliquely, tuberculate scales arranged transversely on the polyp body and internodes lacking ornamentation other than low primary ridges. The genus is divided with morphological and molecular support into two new subgenera, *P.* (*Primnoisis*) and *P.* (*Delicatisis*) but it cannot be confirmed as monophyletic due to the unresolved phylogenetic position of the closely related genus *Notisis* and an undescribed Mopseinae genus. The described species *P. antarctica*, *P. fragilis* plus two new species (*P. chatham* and *P. erymna*) are grouped in *P.* (*Primnoisis*), with shared morphological traits such as perpendicular polyps and large sclerites, with little interspecific molecular variability. *P. rigida, P. delicatula, P. formosa, P. gracilis* (reassigned from *Mopsea gracilis* Gravier, 1913) and two new species (*P. millerae* and *P. niwa*) are grouped in *P.* (*Delicatisis*), with shared morphological traits such as curled polyps and small, narrow sclerites with slightly more interspecific molecular variability.

Three species remain unplaced to subgenus. *P. ambigua* has significant morphological differences from either subgenus, and is currently based on a single, possibly anomalous specimen. *P. mimas* similarly is notably morphologically different to either subgenus and remains tenuously in *Primnoisis* in the hope that future molecular research may be able to elucidate this relationship. Finally, a new species, *P. tasmani,* is positioned basal to all other *Primnoisis* species and the *Notisis* samples. Morphologically it resembles the species in *P.* (*Delicatisis*) but is genetically distant to these specimens. These species remain in *Primnoisis* at this stage as there is no reliable way to exclude them on a morphological basis.

The genus was found to have a circumpolar distribution and to extend into deep temperate waters as far north as 37°S on two continents.

Chapter 4. The biogeography and possible origins of the octocoral genus *Primnoisis.*

4.1 Introduction

The waters around Antarctica harbour an abundance of diverse and unique benthic fauna but the logistics of sampling the deep, cold and isolated habitats have been, and remain, a challenge. Hypotheses on the distributions and origins of much of the Antarctic marine fauna have necessarily been based on haphazard sampling and minimal records, and much biodiversity remains undescribed and unrecognised (Brandt, De Broyer, et al. 2007; Janosik & Halanych 2010). Nevertheless, the increasing use of molecular data from modern collections, especially when combined with geological history, has recently allowed a substantial reshaping of our understanding of biological lineages in Antarctica, their distribution and possible origins.

The geological and hydrological history of Antarctica is thought to have heavily influenced the diversity and population structures of the present day Antarctic marine biota. The fauna has ancient origins from the Gondwana supercontinent, and with its breakup and the beginnings of the strong Antarctic Circumpolar Current (ACC) approximately 31–34 Ma, taxa had to adapt to falling temperatures and increasing glaciations (Brandt 2005). Ancestral traits shared among Antarctic fauna (such as physiological tolerances) have likely influenced resultant distributions of related taxa, but differing evolutionary pressures and vicariant speciation across these vast distances and long time scale has led to a diverse Antarctic fauna with unique niches (Clarke, Johnston, Murphy, & Rodgers 2007). At shorter time scales, it is suggested that numerous asynchronous glacial cycles have helped shape and drive the diversity of Antarctic fauna by isolating communities in upper shelf refugia during localised glacial maxima and forcing adaptations such as eurybathy on some species as available benthic habitat disappeared under ice (Allcock & Strugnell 2012; Barnes & Kuklinski 2010; Janosik & Halanych 2010; Strugnell, Watts, Smith, & Allcock 2012; Thatje et al. 2005).

It has long been understood that the strong ACC which encircles the continent effectively creates an oceanographic barrier for many marine species (Brandt 2005), thus isolating fauna from northern waters but also seeming to aid distribution around the deep continental shelf resulting in apparent circumpolar distributions. However, much of the deep-sea fauna is poorly known with considerable diversity still to be described (Brandt, De Broyer, et al. 2007; Brandt, Gooday, et al. 2007; Gutt et al. 2004) and the biogeographic patterns presented thus far are most likely incomplete or deceptive due to scarcity of sampling in certain areas, the difficulties inherent in deep-sea polar research such as low specimen numbers, and a lack of consideration of the influence of past glacial cycles (Allcock & Strugnell 2012; Janosik & Halanych 2010). Increasingly, recent studies have revealed many fauna that were thought to have a circumpolar distribution actually have limited distributions, with the presence of endemic, cryptic and unrecognised species discovered within many historical species (Baird et al. 2011; Janosik & Halanych 2013; Krabbe et al. 2010; Wilson et al. 2007). However, generalisations cannot be made across faunal groups and even for those species which truly have a 'circumpolar distribution' this may not reflect present day panmixis (Arango, Soler-Membrives, & Miller 2011; Raupach et al. 2010; Strugnell et al. 2012). For example, an ancient sea link between the Weddell and Ross Seas, possibly due to the collapse of the West Antarctic ice shelf as recently as the last few interglacial periods, may explain the strong faunal and genetic links between these two distant seas (Barnes & Hillenbrand 2010; Pierrat et al. 2013) rather than a circumpolar distribution.

The ACC appears to act as an oceanographic barrier to some taxa, resulting in a disjunct fauna between the Antarctic continent and the surrounding subantarctic islands or nearby continental shelves (Allcock et al. 2011; Figuerola, Monleón-Getino, Ballesteros, & Avila 2012; Griffiths et al. 2011; Hoffman, Peck, Linse, & Clarke 2011; Hunter & Halanych 2010; Krabbe et al. 2010; Strugnell et al. 2012) but see Clarke et al. (2005). However, O'Loughlin et al. (2013) reported strong links across the Antarctic convergence at a genus level, with only 10 of the 55 known holothurian genera in Antarctica recorded as endemic, and argued the strong current is less of a barrier to deeper-dwelling taxa. There is evidence that the benthic communities of the Antarctic continental shelf or those on subantarctic islands south of the ACC act as founder populations or diversity hotspots radiating into the Southern Ocean (Allcock et al. 2011; Briggs 2003; Griffiths et al. 2011; Linse, Cope, Lörz, & Sands 2007). Griffiths et al. (2011) found the highest diversity of pycnogonids on the South Shetland Islands and suggested it was a centre of radiation for the southern hemisphere and a possible refuge from glaciations and, similarly, the octopus genus *Pareledone* was found to be most diverse at the South Shetland islands (Allcock et al. 2011). Other taxa such as penguins, molluscs and echinoderms have been noted as radiating northward from Antarctica, possibly assisted by the movement of the cold, abyssal water (Briggs 2003and references within).

In contrast, some taxa have been recorded moving into Antarctica. The Scotia Arc and other subantarctic islands near the Antarctic peninsula can act as a link for South American taxa into Antarctica which are then transported in an east-west direction around the continent (Griffiths et al. 2009) although Pierrat et al. (2013) suggested this connection is not consistent for all taxa. Brandt (2005) suggested that if the cold, north-flowing Antarctic Deep Water (ADW) ceased during interglacial periods, temperate deep-sea fauna may have been able to migrate into Antarctica, and some recent records of North Atlantic adult spider crabs and brachyuran crab larvae south of the ACC indicate contemporary movement of taxa across the current (Briggs 2003).

Nevertheless, contemporary movement of taxa across the ACC appears limited. Wilson (2009) recorded the nudibranch *Doris kerguelenensis* on either side of the Drake Passage, but the specimens from South America, present in three different parts of the phylogenetic tree, were always positioned in a separate clade to their sister taxa from the Antarctic continent. The species appears to have bridged the Drake Passage numerous times and relatively recently, but once bridged is sufficiently isolated to diverge into a separate lineage. Additionally, O'Loughlin et al. (2013) found that some nominal species of holothurians recorded either side of the Antarctic convergence contained separate 'ESUs' (Evolutionary Significant Units) which were separated genetically and geographically across the convergence. In a comparison of geographic regions north and south of the ACC, Griffiths et al. (2009) found that New Zealand fauna did not overlap with Antarctic or South American species at all, despite the temperate regions such as New Zealand, Tasmania and South Africa being identified as "species generation/radiation hotspots" for gastropods, bivalves and cheilostomata with more genera than areas south of the ACC. This would suggest current species do not bridge the ACC, at least in eastern Antarctica, which lacks a linking island chain with temperate waters.

The disjunction between fauna from the subantarctic islands around New Zealand and that of the Antarctic continent on the eastern side of the continent seems to be pronounced due to much greater isolation and earlier separation from the Gondwana mainland (Griffiths et al. 2009; Pierrat et al. 2013). Despite this evidence of distinct bioregions in subantarctic New Zealand and Antarctica, one apparent link between the Australian and New Zealand fauna and the Antarctic are the Notothenioid fishes, with their distinctive antifreeze glycoproteins (AFGPs). This lineage is thought to have diverged from an ancestor on the southern Australian coastline, probably at the time of the separation of the Antarctic and Australian landmasses (Matschiner, Hanel, & Salzburger 2011; Rogers 2007). Endemic genera of fish in Australia are phylogenetically basal to the closely related Notothenioids but lack the physiological adaptation of antifreeze proteins, suggesting that with the innovation of the AFGPs the Notothenioids could extend and diversify on the Antarctic continental shelf, exploiting this niche as the water temperature around Antarctica decreased. Additionally, Fraser et al. (2009) showed that after ice scour at the Last Glacial Maximum (LGM), bull kelp from refuges north of the winter sea ice extent recolonised south to subantarctic islands right round the Antarctic continent. The refuges were most likely the islands south of New Zealand and not the linking islands of the Scotia Arc and the South American continent (Fraser et al. 2009).

Octocorals are a common and obvious part of the benthic fauna on the Antarctic and high-latitude continental shelves and subantarctic islands. Few studies have investigated the phylogeography of octocoral species in or near Antarctica, with most recent papers attempting to clarify the taxonomic confusion within some commonly occurring taxa or describing new species (e.g. Taylor et al. 2013; Zapata-Guardiola & López-González 2012). The distribution of a few octocoral species are well studied, such as *Paragorgia arborea,* which has a wide-spread deep-sea distribution (excluding Antarctica) and can contribute to understanding the evolution of deep-sea taxa (Herrera et al. 2012). However, most other octocoral groups are poorly defined with substantial taxonomic rearrangement and review required before these groups can be confidently used in biogeographic analysis (Baco & Cairns 2012; McFadden & van Ofwegen 2013). As such there have been restricted opportunities to map true distributions of octocoral groups and thus predict and interpret influences on deep-sea octocoral distributions, although this situation is improving (Baco & Cairns 2012; Herrera et al. 2012; McFadden & van Ofwegen 2013; Pante et al. 2012; Thoma et al. 2009). It has often been assumed that octocorals, as common seamount fauna, have restricted, endemic distributions. However, genetic data has recently revealed the same haplotypes exist across very large distances, even different oceans (Herrera et al. 2012; Thoma et al. 2009) suggesting much wider distributions of some taxa, although which taxonomic level is represented by these haplotypes (e.g. genus) is not clear (Baco & Cairns 2012). Depth may also be significant in determining distribution as stratified water masses can isolate populations vertically and limit genetic connectivity (Baco & Cairns 2012; Miller et al. 2011; Prada & Hellberg 2013).

Primnoisis is an octocoral genus thought to be restricted to higher southern latitudes with the most northerly collection at approximately 38°S on the Australian continent and 37° on the South American continent. It is found at depths between 100–2000 m, and is relatively common at depths of 200–800 m on the Antarctic continent (Chapter 3). Most records of the genus describe new species (Bayer & Stefani 1987b; Gravier 1913; Hickson 1907; Kükenthal 1912; Wright & Studer 1889) although *Primnoisis antarctica* was found to be an early coloniser after ice scour (Arntz & Gutt 1999; Teixidó, Garrabou, Gutt, & Arntz 2004) and it was included in a study of the role of plankton communities in its diet (Orejas, Gili, & Arntz 2003). This species was thought to have a circumpolar distribution as the original collection was from Prince Edward Island and subsequent records were from many places on the Antarctic continent (Arntz & Gutt 1999; Bayer & Stefani 1987b; Branch & Williams 1993; Grant 1976; Gravier 1913). However, identification of *P. antarctica* is incorrect in some of these cases and questionable in others (Chapter 3), and the species is most likely confined to the waters around Prince Edward Island in the southern Indian Ocean. It is likely that the genus *Primnoisis* has a circumpolar distribution that extends to many subantarctic islands. Little is known of the reproductive mode in this genus but it is thought to brood larvae (Teixidó et al. 2004), which would suggest long-distance larval dispersal and connectivity across oceanic distance would be less likely than for a broadcast spawning species (Jackson 1986) and we might predict that allopatric speciation in a group with limited dispersal could lead to local endemic species within the genus.

This study combines distribution and phylogenetic data from *Primnoisis* species with an aim to (i) explore the distribution of species and the possible origin of the genus given it was traditionally assumed to have an essentially Antarctic and subantarctic distribution (Alderslade 1998) but has now been recorded numerous times in temperate waters; (ii) determine the degree of connectivity or isolation of populations of the wide-spread species *P. fragilis* on the Antarctic continent using two mitochondrial gene regions; and (iii) assess the influence of depth on distribution at both the genus and species level.

4.2 Methods

4.2.1 Sample collections

Samples were collated from recent voyages and from preserved museum specimens, and were from numerous locations (Fig. 4.1 & Chapter 3). A total of 171 *Primnoisis* specimens were examined and identified based on morphology and phylogenetic clades. Older specimens from museum collections included: type material from Prince Edward Islands, off the coast of Rio de le Plata, Argentina, and from McMurdo Sound from the National History Museum (NHM); type material from Marguerite Bay from the Muséum national d'Histoire naturelle (MNHN); type material from South Georgia Island from the National Museum of Natural History (NMNH) and historical material from Prydz Bay and the Knox Coast from the Australian Museum (AM), South Australian Museum (SAM) and Museum Victoria (MV). If original coordinates were not available they were estimated in Google Earth from collection location descriptions. Records of *Primnoisis* from the literature were not included unless the specimen was available for examination as a recent taxonomic review found a number of inaccurate determinations in the literature (Chapter 3).

Recently collected specimens were from sites around Antarctica including Commonwealth Bay, Tressler Bank, Wilhelm II Land, Heard Island, Dumont d’Urville, Ross Sea, Balleny Islands, Macquarie Island, Chatham Rise, Tasmanian seamounts and Scotia Arc (Fig. 4.1). These samples were collected with the assistance of CSIRO, MNHN, NIWA, AAD and SIO and specific details of samples included are in Chapter 3, section 3.3.2. DNA sequencing of the mtMutS and igr1–COI mitochondrial gene regions was attempted only on the recently collected specimens.

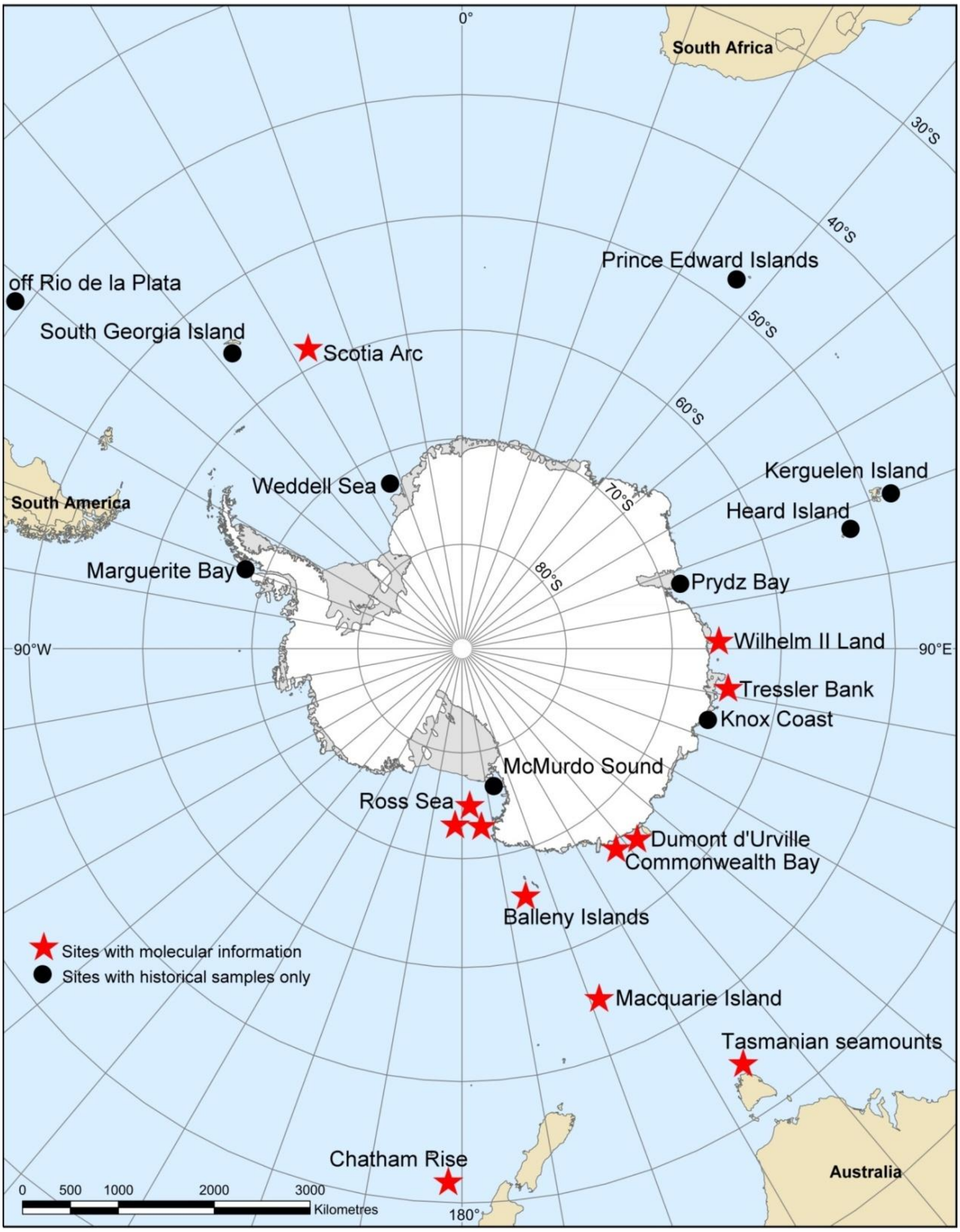


Figure 4.1. Map of Antarctica showing the sample collection locations (see Chapter 3, section 3.3.2 for site details). Based on Map 13351 courtesy of the Australian Antarctic Division.

4.2.2 Species distributions

For each species, sample sites of all available specimens were mapped onto Map 13011 from the Australian Antarctic Division (AAD) using Ulead PhotoImpact 12 image software in order to assess the distribution of each species. This map includes an estimation of the position of the Antarctic Circumpolar Current (ACC), the Polar Front, and minimum and maximum extents of the sea ice providing an overview of key physical factors that might influence distribution.

4.2.3 Genetic data collection and phylogenetic analysis

Two mitochondrial gene regions, mtMutS and igr1–COI were sequenced for the recently collected specimens (see Chapter 3, section 3.2.5 for detailed methods) and used for phylogenetic reconstructions for cladistic assessment of species groupings and ancestral relationships. Sequences were assessed for the most appropriate phylogenetic model in JModelTest v2.1.4 (Darriba et al. 2011) with default settings (TPM1uf+G for mtMutS and TVM+I for igr1–COI) and the closest available model was implemented for phylogenetic reconstruction (GTR+G and GTR+I respectively). Using the two gene regions concatenated, Bayesian analysis conducted in the software package MrBayes v.3.1.2 (Huelsenbeck & Ronquist 2001) was employed to construct a phylogenetic tree (priors were adjusted accordingly to implement the appropriate model). The Markov Chain Monte Carlo (MCMC) analysis was run with 2 runs, 4 chains, sample frequency of 100 and a burn-in of 25%. Analyses were run for the number of generations required to achieve an average standard deviation of split frequencies of 0.002 between the two runs.

Specimens from the closely related genus *Notisis* and a specimen morphologically determined to be from an undescribed Mopseinae genus (Alderslade pers. comm.) were sequenced and included as outgroups. These specimens proved to have an entwined relationship with *Primnoisis* specimens, thus additional sequences from the (nominally sister) genus *Keratoisis* (GenBank EF060025 and GU933628) were also included as an outgroup. Phylogenetic trees were viewed and prepared for publication in FigTree v1.3.1 (Rambaut 2006-2009).

4.2.4 Population structure analysis

For species that were found to have a circumpolar distribution, analysis of haplotype diversity and distribution was conducted to explore allopatric groupings and population structuring. Only *P. fragilis* had sufficient samples (n= 25) across multiple locations for statistical comparison of genetic differentiation among geographically isolated populations and to test the hypothesis of ongoing gene flow between these populations. The analysis was performed by Analysis of Molecular Variance (AMOVA) on the concatenated gene regions using the distance matrix option in Arlequin v3.5.1.3 and statistical significance was assessed on 10 000 permutations with a significance level of $p<0.05$.

4.2.5 Depth and distribution of *Primnoisis*

Many deep-water species are often stratified by depth and this likely plays an important role in speciation and diversification. In an attempt to quantify 'presence/absence' of *Primnoisis* in relation to depth, all sample depths of benthic trawls and sleds from 16 voyages (all of which collected *Primnoisis* at some, but not all, sites) were collated into 400 m depth intervals (with the intervals based on preliminary data exploration) and expressed as a percentage of total trawls for the voyage. Against this representation of sampling effort, the number of *Primnoisis* samples present in each depth interval is expressed as a percentage of total *Primnoisis* samples collected to demonstrate at which depths *Primnoisis* is most prevalent. Chi-square tests were conducted within the depth ranges to test the null hypothesis that there is no statistical difference in *Primnoisis* occurrence by sampling effort either side of the ACC. Additionally, depth records for each species were plotted in 100 m depth intervals to explore possible depth stratification at as fine resolution as possible given the depth accuracies of trawling.

4.3 Results

4.3.1 Overall species distributions

Species found within *Primnoisis* had a range of distribution patterns, with some species appearing to be circumpolar while others have very localised distributions (Table 4.1 and Figs. 4.2–4.6). Notably, sample size of some species was very limited and there remain large areas of the Antarctic continental shelf and many subantarctic islands with no confirmed records of *Primnoisis* so it is likely that these results underestimate the diversity and distribution of species within the genus.

Table 4.1. *Primnoisis* species found showing number of specimens, number successfully sequenced and their distributions.

Subgenus	Species	No. examined	No. sequenced for both loci	Distribution
Primnoisis	*antarctica*	2	0	Prince Edward Island
	cf. *antarctica*	14	0	Heard Island plateau
	fragilis	35	20	Wilhelm II Land, Commonwealth Bay, Tressler Bank, Balleny Is., Ross Sea, Prydz Bay, Scotia Arc
	chatham	6	3	Chatham Rise
	erymna	5	2	Macquarie Ridge, Chatham Rise
Delicatisis	*rigida*	1	0	off Rio de la Plata, Argentina
	delicatula	2	1	McMurdo Sound, Dumont d'Urville
	formosa	20	8	Marguerite Bay, Wilhelm II Land, Tressler Bank, Knox Coast, Commonwealth Bay, Dumont d'Urville, Ross Sea, Balleny Islands
	gracilis	23	5	Marguerite Bay, Weddell Sea, Wilhelm II Land, Tressler Bank, Commonwealth Bay, Prydz Bay, Ross Sea
	millerae	9	2	Ross Sea, Knox Coast
	niwa	19	4	Macquarie Ridge
Unplaced	*ambigua*	1	0	Kerguelen Island
Unplaced	*mimas*	3	0	South Georgia Island
Unplaced	*tasmani*	30	5	Tasmanian seamounts
Totals		170	50	

There was a clear pattern of spatial segregation of species found north of the ACC with most species endemic to certain regions or found only in one or two locations. In contrast, most species found south of the ACC were widely distributed around the Antarctic continent (Figs. 4.2–4.6). Many specimens originally determined as *P. antarctica* in the literature were here found to be specimens of *P. fragilis,* which was common and widespread in the recent collections as well. This species has an extensive distribution around the Antarctic continent (Fig. 4.2), including recently collected specimens from the Scotia Arc which were found to share a haplotype with specimens from east Antarctica (see below).

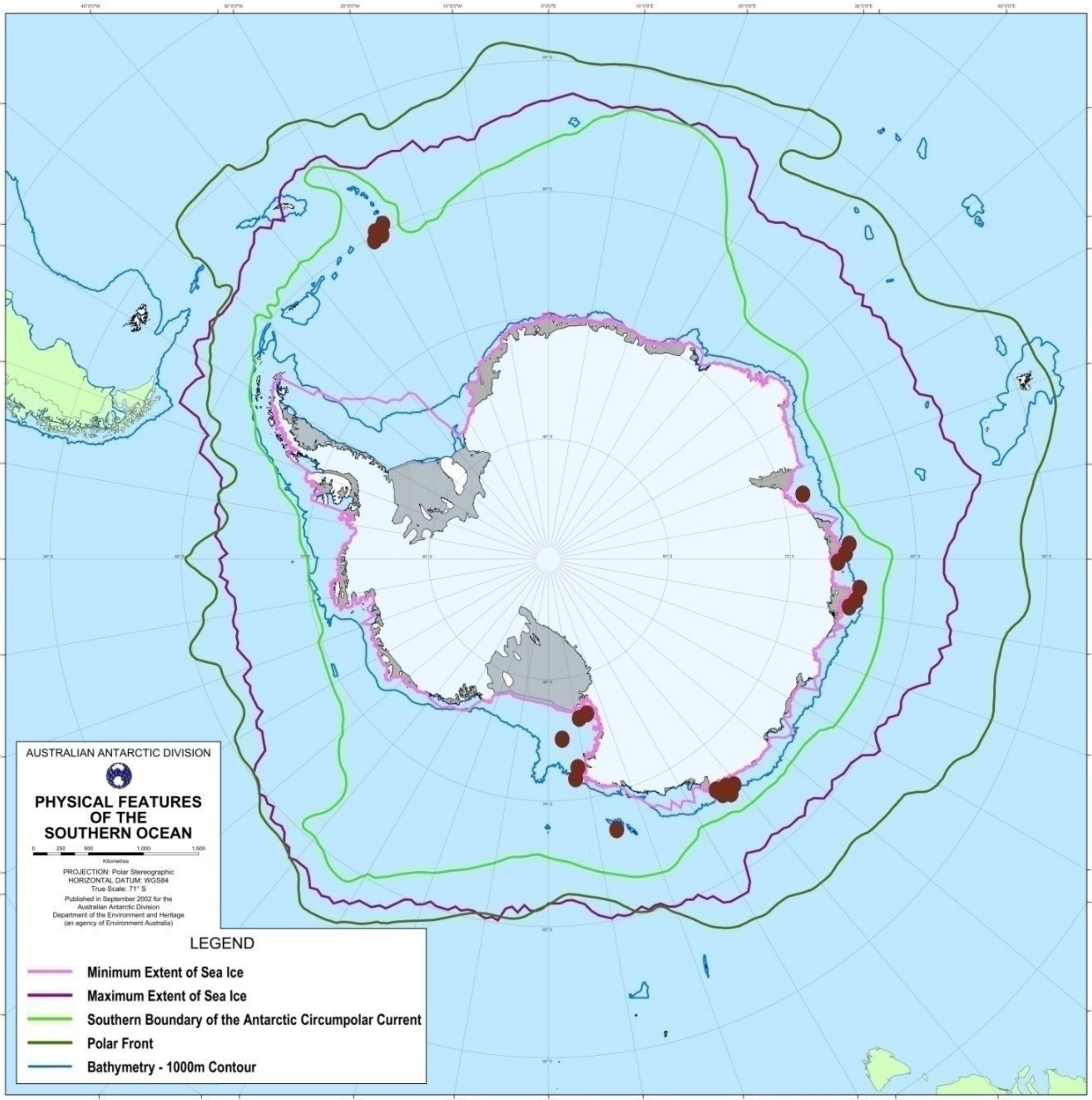


Figure 4.2. Distribution of *Primnoisis fragilis*.

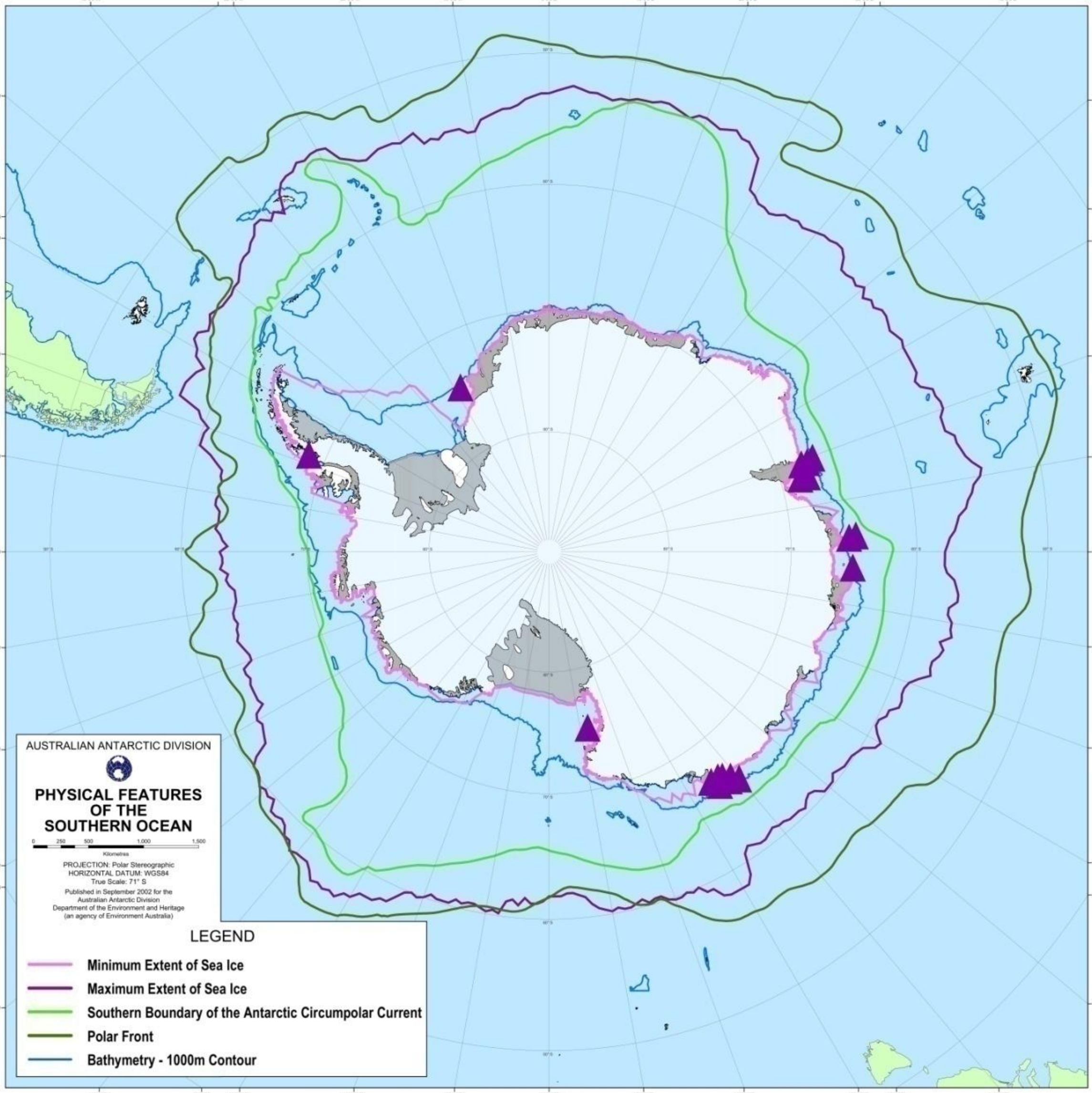


Figure 4.3. Distribution of *Primnoisis gracilis.*

Two other species (*P. gracilis* and *P. formosa*) were also found at multiple sites spread around the Antarctic continental shelf (Figs. 4.3; 4.4), although most of the samples available for examination were from the eastern Antarctic continental shelf. The type specimens were the only material of *P. formosa* available from the Antarctic peninsula and similarly, the type material from the peninsula plus another small specimen from the Weddell Sea was the only west Antarctic material available for *P. gracilis*.

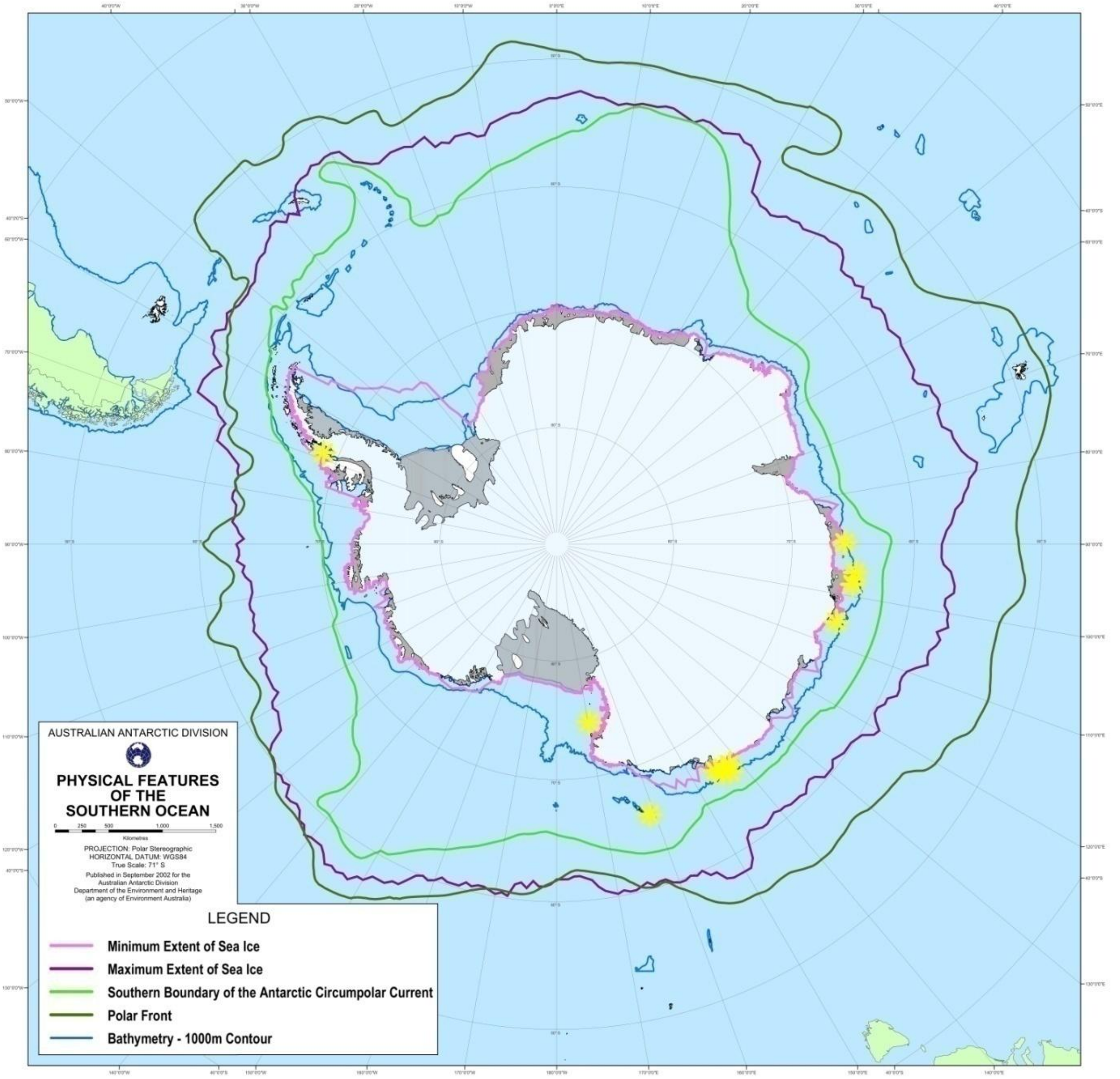


Figure 4.4. Distribution of *Primnoisis formosa.*

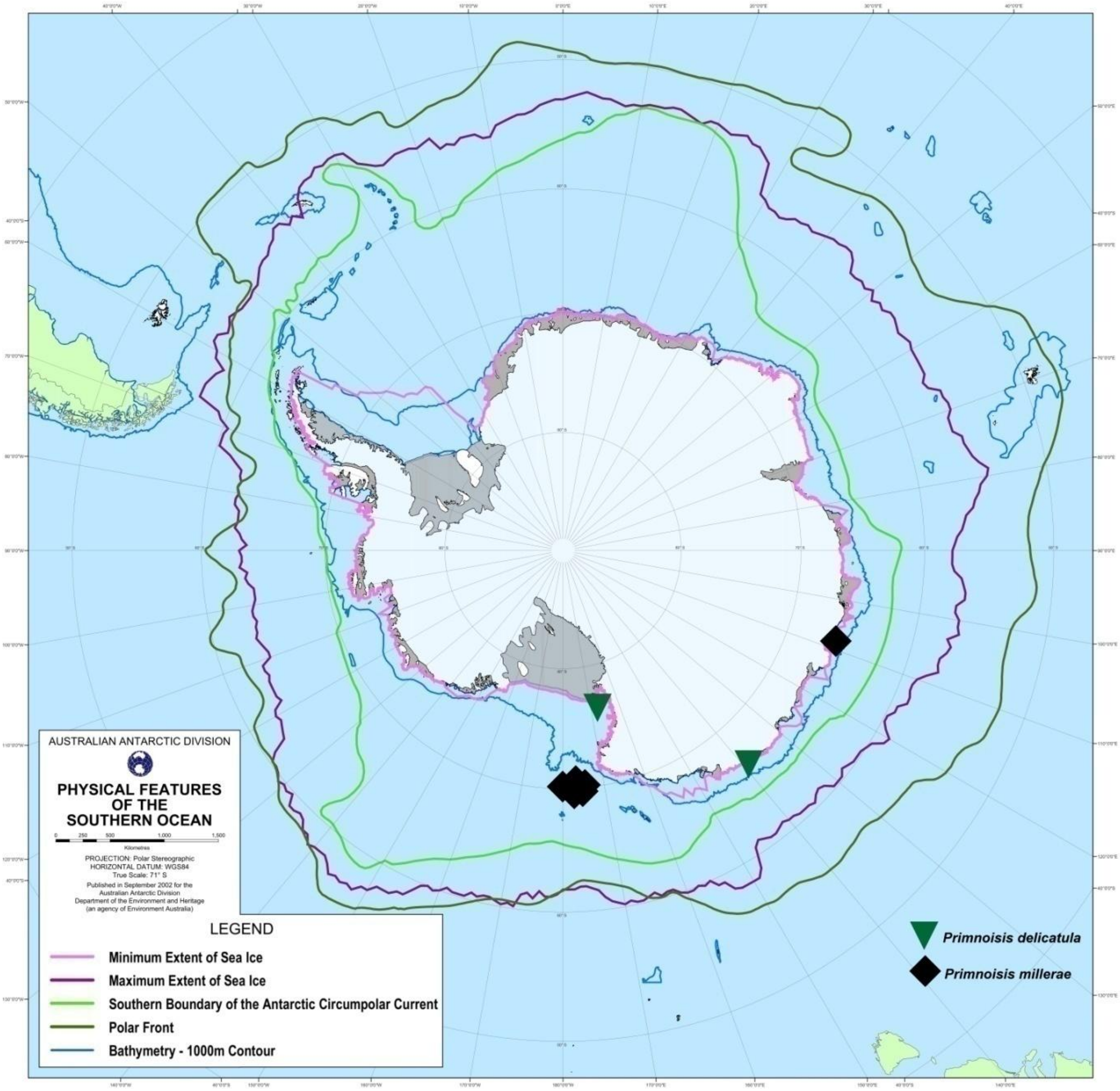


Figure 4.5. Distributions of *Primnoisis delicatula* and *P. millerae.*

P. delicatula and *P. millerae* were recorded from two geographically separated sites on the east Antarctic coast, suggesting broad distributions (Fig. 4.5). However, *P. delicatula* is only recorded from two isolated occurrences—the type specimen collected in 1903 from McMurdo Sound, and one recently collected specimen from Dumont d'Urville (Fig. 4.5) so inferences about its broader distribution must be treated with caution. Recently collected specimens of *P. millerae* were restricted to a small area adjacent to the Ross Sea, but one additional specimen was collected in 1914 off the Knox Coast. Interestingly, the group of specimens from the Ross Sea are all from deep waters (>800 m) and the Knox Coast specimen is one of very few historical specimens collected on the Antarctic coastline at deeper than 1500 m. *P. millerae* may have an extensive distribution but at greater depths than those usually sampled. Future work is needed to be able to confirm the presumed presence of this species at intervening sites or deeper waters.

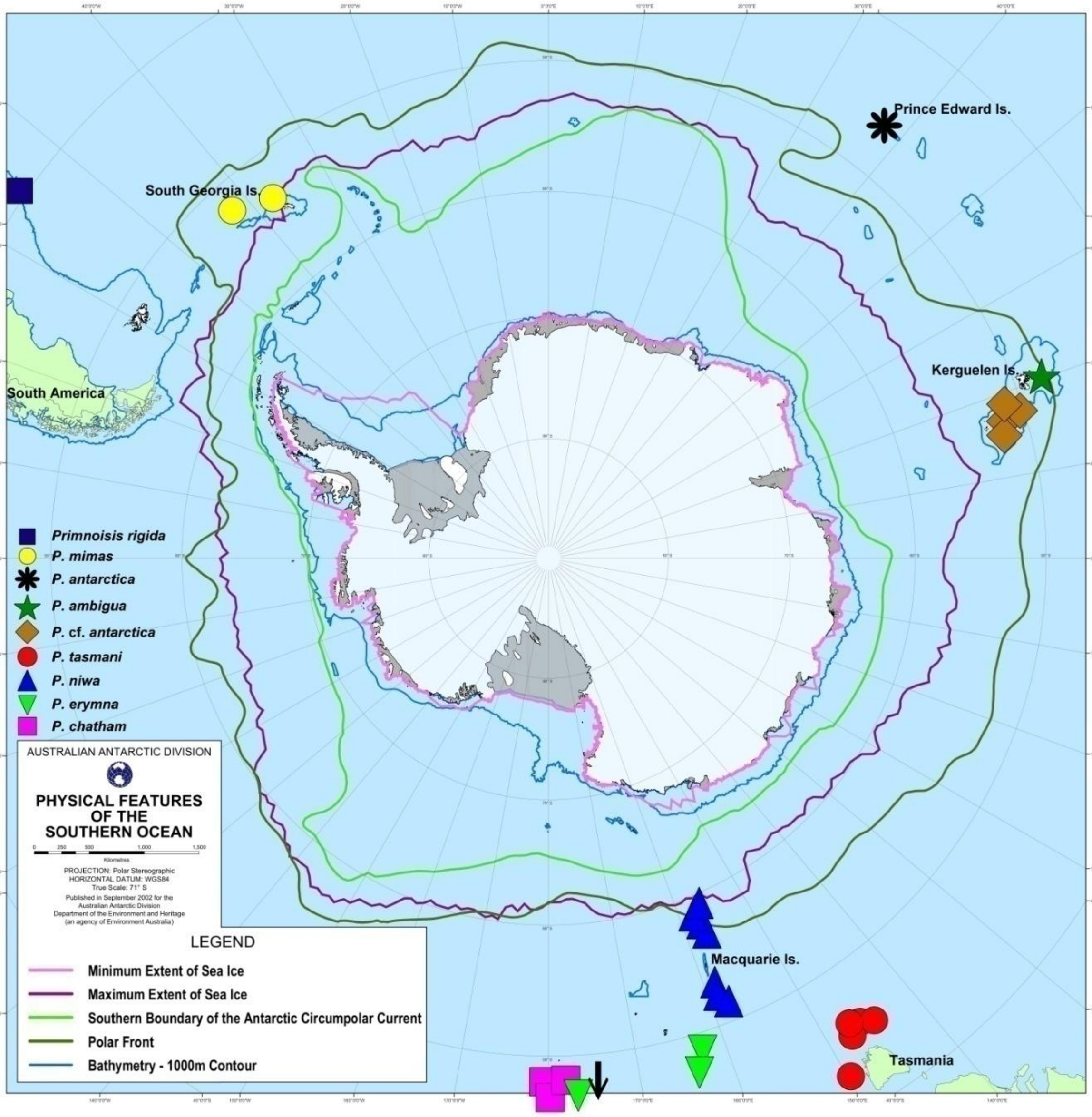


Figure 4.6. Distributions of *Primnoisis rigida, P. mimas, P. antarctica, P. ambigua, P.* cf. *antarctica*, *P. tasmani, P. niwa, P. erymna*, *P. chatham.*

P. antarctica was found to be very restricted in distribution and not commonly occurring on the Antarctic continent as assumed from the literature—in fact, for this species the only material available was the type material (collected 1887) from near Prince Edward Island (Fig. 4.6). Numerous specimens collected on the Heard Island plateau were grouped as an indeterminate complex named *P.* cf. *antarctica* due to some morphological similarities to that species (Fig. 4.6). Unfortunately, none of these specimens were successfully sequenced but future molecular work may be able to elucidate this relationship. *P. ambigua* has only been recorded once, from the waters near Kerguelen Island, the only record of *P. rigida* remains the type specimen collected from deep water off the coast of Rio de la Plata, Argentina and the records of *P. mimas* are from three specimens at or near the type locality, South Georgia Island (Fig. 4.6). Four species, *P. chatham,* *P. erymna, P. niwa* and *P. tasmani,* have restricted distributions and appear to be endemic to subantarctic ridges or seamount features (Fig. 4.6) south of Australia and New Zealand.

The species recorded north of the ACC appear to be endemic to key areas (Fig. 4.6) but some of these species consist of very few records. However, the species *P. tasmani, P. niwa, P. erymna, P. chatham* and *P.* cf. *antarctica* were all common in collections (Table 4.1) but were still restricted in distribution, suggestive of endemism. Well over 400 hauls were conducted at these sites and there was almost no record of any of these species outside each specific area. *P. erymna* was the only species found in more than one area, with a single specimen collected from the Chatham Rise east of New Zealand as well as from Macquarie Ridge. This species is closely related to *P. chatham*, sharing a haplotype and from similar geographical areas but with clear morphological differences (Chapter 3). There is evidence of other octocoral species also occurring on both the northern Macquarie Ridge and Chatham Rise (Luisa Dueñas, unpublished data), and Miller et al. (2010) found no genetic difference between populations of the scleractinian corals, *Desmophylum dianthis* and *Solenosmilia variabilis* collected from Chatham Rise and Macquarie Ridge, suggesting a close link between these oceanographic features probably facilitated by the dominant water bodies and currents (Miller et al. 2010).

4.3.2 Congruence of distributional patterns and molecular groups

Many specimens could not be successfully sequenced, probably due to DNA degradation of these delicate coral colonies (Miller et al. 2010). However, for those that were successfully sequenced, there was congruence between the molecular clades and the geographical distribution patterns found for the morphological groups. Two deep divisions were consistently found in the phylogenetic analysis—*P. tasmani* samples were basal to all other *Primnoisis* samples, while the remaining samples split into two distinct groups, labelled as subgenera *P.* (*Primnoisis*) and *P.* (*Delicatisis*) (Fig. 4.7). Both subgenera contained species recorded north or south of the ACC.

4.3.2.1 South of the ACC

All *P. fragilis* samples formed a well-supported clade that included sequences from six widely separate sites including those from Scotia Arc (Fig. 4.7). These sites are across vast distances from Wilhelm II Land/Tressler Bank, the Ross Sea and Scotia Arc and are all south of the ACC including the Scotia Arc where the bulk of the ACC is predicted to skirt north of the arc. The clade consists of four haplotypes which only differ by 1–2 nucleotides across the concatenated gene regions. These haplotypes have some minor geographic structuring (see below).

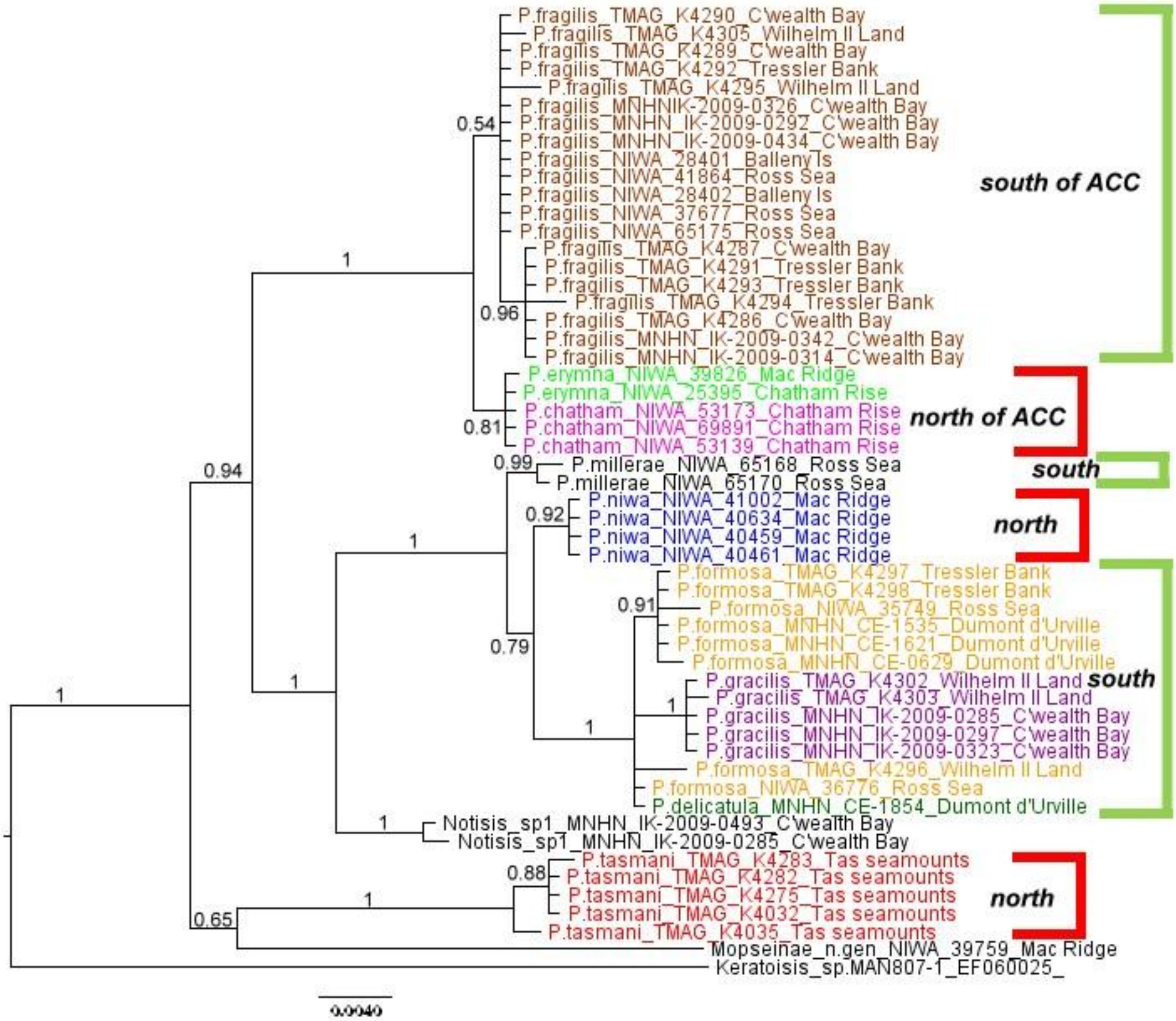


Figure 4.7. Bayesian phylogenetic reconstruction from nucleotide sequences for the two mitochondrial regions mtMutS and igr1–COI concatenated. Numbers shown are posterior probabilities (partitioned model, 8000000 generations, burnin=20000, split freq=0.002, PSRF 1.000-1.001). The colours of clades match the colours marking distributions in the maps above.

Other specimens also formed well supported clades with material from widely separated sites (Fig. 4.7). A single haplotype of *P. formosa* was shared across the eastern Antarctic sites (Tressler Bank, Commonwealth Bay and Ross Sea) and with two samples falling outside the clade with differences of 1–3 nucleotides. *P. gracilis* samples formed a well-supported clade with a single haplotype found at Wilhelm II Land and Commonwealth Bay. The suspected wide distributions of the two other species, *P. delicatula* and *P. millerae,* found within the ACC (Fig. 4.5), could not be confirmed due to low sample numbers. *P. millerae* samples formed a single clade, but these samples were all collected from the relatively small geographic area off the Ross Sea, and *P. delicatula* was represented by a single specimen in the molecular phylogeny which only differed from the *P. formosa* haplotype by a single nucleotide.

4.3.2.2 North of the ACC

The species *P. chatham* and *P. erymna* shared a haplotype across both gene regions and are closely related to *P. fragilis*, which is found south of the ACC (Fig. 4.7). The sharing of a haplotype between the two northern species reflects the relative proximity of their populations (Fig. 4.6) and the likely faunal link between Macquarie Ridge and Chatham Rise. In the other subgenus *P .niwa* formed a well-supported, consistent clade with the samples all collected from the Macquarie Ridge. Interestingly, it is most closely related to *P. millerae,* which is found south of the ACC.

Specimens of *P. tasmani* from the seamounts south of Tasmania and the continental shelf east of Tasmania formed a clade basal to all other specimens (Fig. 4.7) and were the northern-most population studied. They are morphologically very similar to species on the relatively distant *P.* (*Delicatisis*) branch and differ substantially from the species on the *P.* (*Primnoisis*) branch. Thus the internal relationships among these *Primnoisis* species remain unresolved, with incongruence between morphological and molecular relationships, and this species is unplaced at the subgenus level. Additionally, the *P. tasmani* clade was also basal to the two specimens of the closely related genus *Notisis* and formed a sister clade with the specimen of an undescribed Mopseinae genus, indicating that *Primnoisis* may be polyphyletic.

4.3.3 Population structure within *P. fragilis*

Twenty five specimens of *P. fragilis* were sequenced from six locations (Wilhelm II Land, Tressler Bank, Commonwealth Bay, Balleny Islands, Ross Sea and Scotia Arc). Four haplotypes were found for the concatenated gene regions, with most occurring at more than one location (Table 4.2 and Fig. 4.8). The four haplotypes only differed by one or two nucleotides (0.06–0.11%) across the concatenated sequences (1718 bp long).

Table 4.2. Presence of *P. fragilis* haplotypes at six sample sites around Antarctica. Sites are listed in clockwise geographical order, n column = number of samples from each site; n row = number of times each haplotype was recorded.

Sites in clockwise order		Haplotypes			
		H1	H2	H3	H4
	n	7	10	7	1
Wilhelm II Land	2	2			
Tressler Bank	4	1		3	
Commonwealth Bay	9		5	4	
Balleny Islands	2	2			
Ross Sea	3	2	1		
Scotia Arc	5		4		1

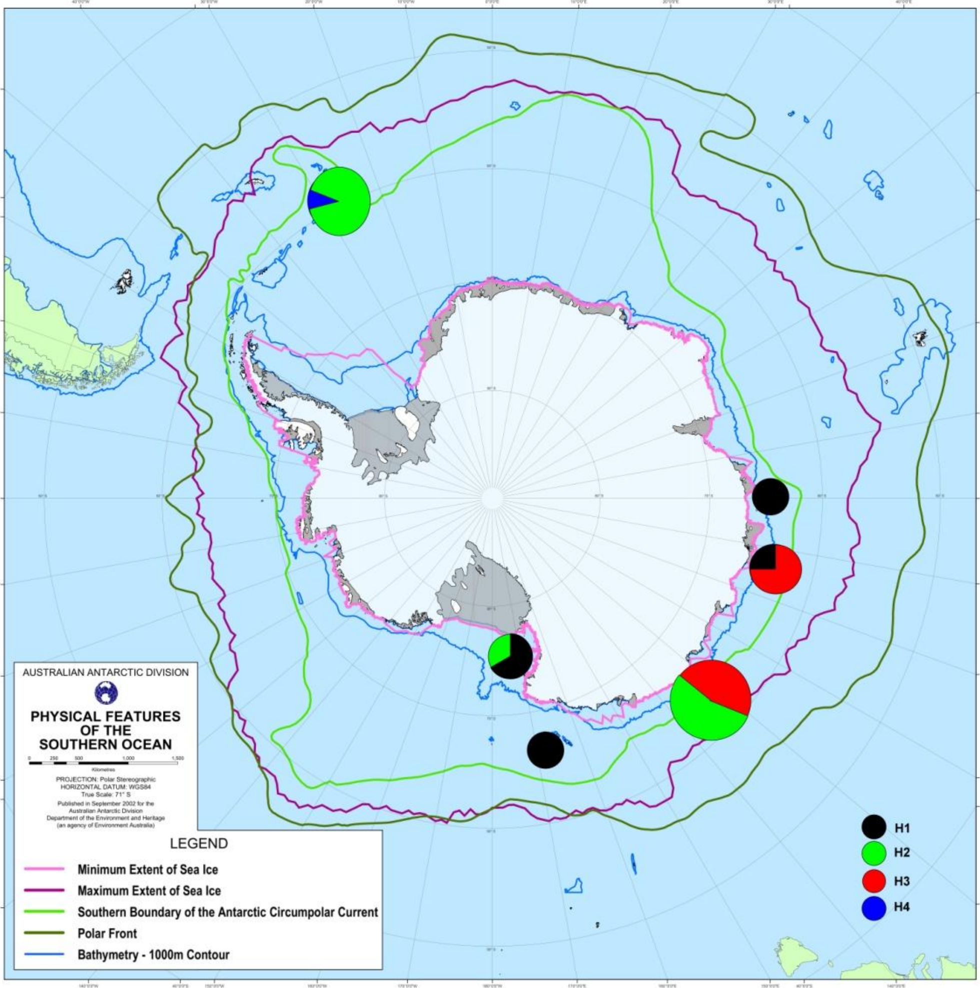


Figure 4.8. *Primnoisis fragilis* haplotype distributions around the coast of Antarctica.

There was a tendency for adjacent locations to share haplotypes, although H1 was not collected from Commonwealth Bay nor H2 from Balleny Islands, but this is possibly just an artefact of limited sampling. A single haplotype (H2) was shared between Commonwealth Bay, Ross Sea and Scotia Arc—a distance of approximately 7000 km and another haplotype (H1) was shared from Wilhelm II Land to the Ross Sea—a distance of approximately 4000 km.

AMOVA results based on the concatenated gene regions of *P. fragilis* samples were equivocal, showing a significant pairwise F_{ST} value between the east Antarctic sites (Wilhelm II Land/Tressler and Balleny Is/Ross Sea) and Scotia Arc, but not between the Scotia Arc and Commonwealth Bay (Table 4.3). This is largely due to the similar frequency of Haplotype 2 between these two latter sites. Neither of the haplotypes found at the Wilhelm II/Tressler Bank combined site were recorded at Scotia Arc suggesting limited gene flow between these vastly separated sites. In general, there is some indication that the Scotia Arc is different to the east Antarctic sites and little evidence of other population structure within the species, although these results are constrained by very small sample numbers and no more than two haplotypes occurring at any one site. Significant F_{ST} values are an indication of pronounced differences in allele frequencies between populations (Freeland, Kirk, & Peterson 2011) so with such low numbers of alleles and samples these significant F_{St} results are an indication only.

Table 4.3. Pairwise F_{ST} values between *P. fragilis* collection sites as determined by analysis of molecular variance. * p<0.05

	n	1	2	3	4
Wilhelm II/Tressler	6	—			
Commonwealth Bay	9	0.0451	—		
Balleny Is/Ross Sea	5	0.2411	0.5071*	—	
Scotia Arc	5	0.3002*	0.2401	0.5000*	—

4.3.4 Depth structuring within the genus

Depth structuring was apparent across the genus with species north of the ACC found disproportionately at depths >600 m, while south of the ACC specimens were largely at depths shallower than 600 m (Fig. 4.9A, B). Those species north of the ACC appear to occur disproportionately at the 600–1000 m depth range as just 16% of the sampling effort at this depth resulted in 43% of the *Primnoisis* specimens (Fig. 4.9A). Trawls north of the ACC were concentrated in the 1000–1400 m depth range with over 40% of hauls producing 37% of *Primnoisis* specimens*,* suggesting further sampling at between 1000 and 1400 m would likely expand the recorded distribution of *Primnoisis.* North of the ACC there were few records of *Primnoisis* in waters shallower than 600 m with only 11% of the specimens recorded from 20% of the sampling effort. No specimens were recorded from waters <200 m (Fig. 4.9A).

South of the ACC, 52% of the sampling was between 200–600 m depth, however more than 70% of the *Primnoisis* samples were collected from those depths (Fig. 4.9B). In comparison, between 600–1000 m, 30% of the sampling effort only resulted in 13% of the *Primnoisis* samples collected. Only four specimens (interestingly all *P. millerae*) were collected at depths >1000 m south of the ACC and these were from commercial voyages. Total voyage depth data could not be included in this analysis so the specimens were excluded from the percentage analysis. There were very few deep (>1000 m) samples in the voyage data available from south of the ACC and this habitat remains to be properly assessed for the presence of *Primnoisis* species. At depths <200 m, sample effort (10%) was similar to the percent of *Primnoisis* records at those depths (15%), suggesting a relatively under-explored habitat for the genus.

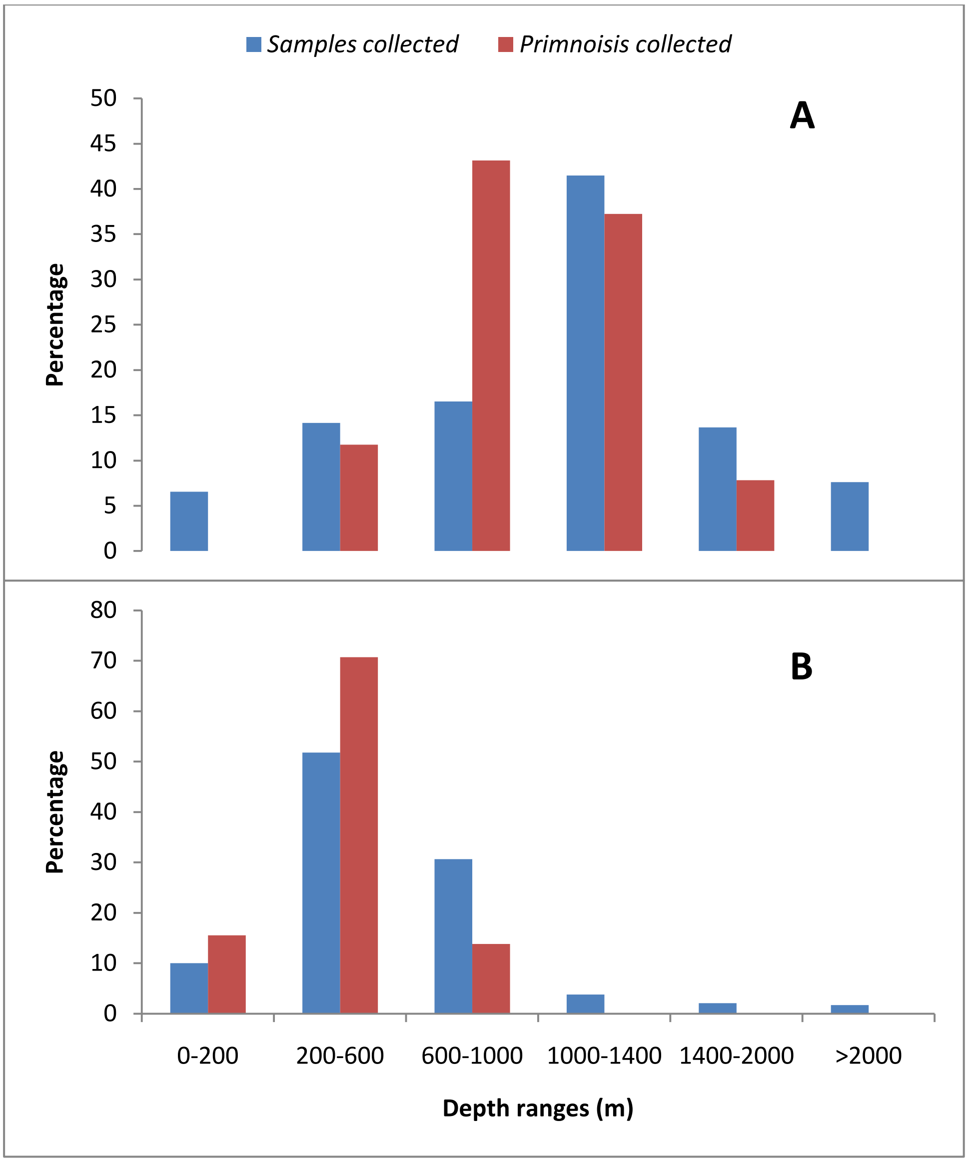
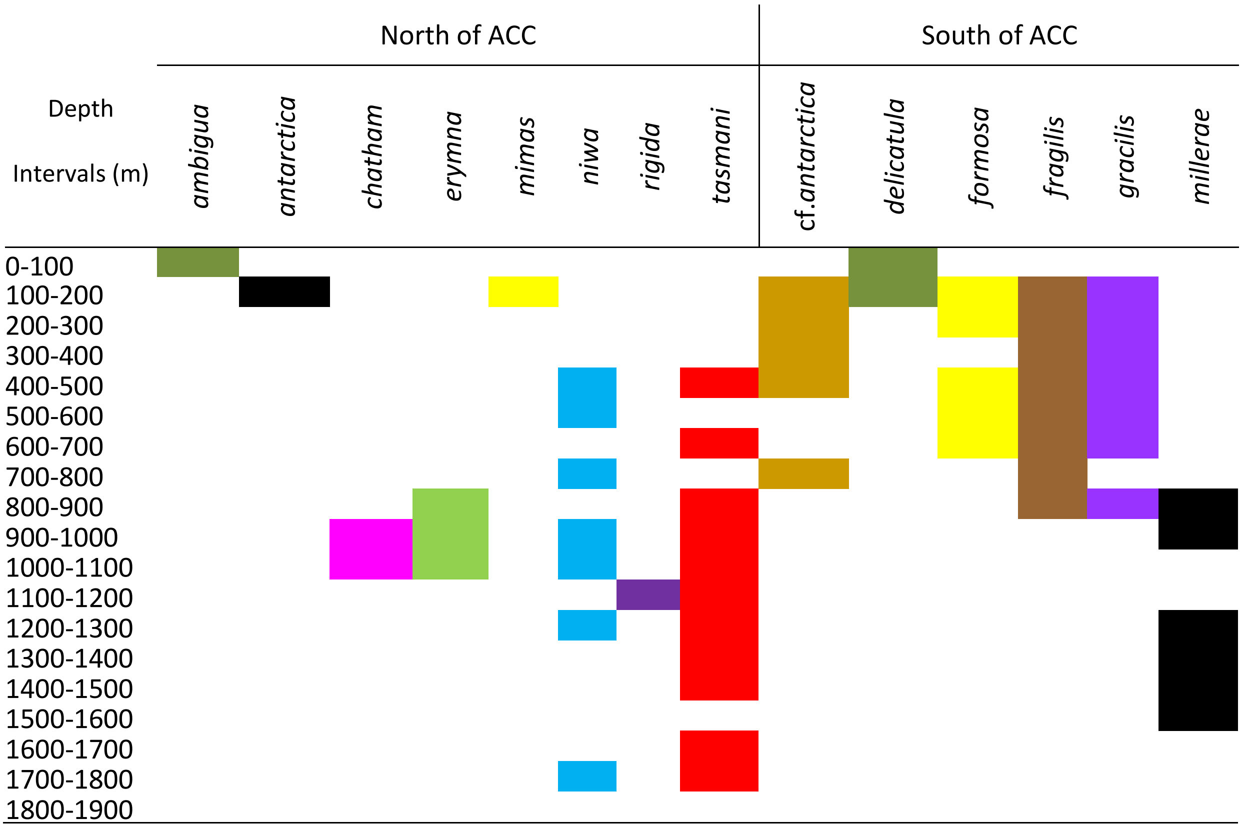


Figure 4.9. Percentage of all samples collected and *Primnoisis* recorded at average depth ranges from 16 voyages, separated into those north (A) and south (B) of the Antarctic Circumpolar Current.

Chi-squared tests conducted at each depth range indicated within two depth ranges there is a significant difference between north and south of the ACC in the observed occurrence of *Primnoisis* by sampling effort (0–200 m (p= 0.028) and 600–1000 m (p= 2.845^{-09})). Thus north of the ACC *Primnoisis* specimens were statistically more likely to be collected in the 600–1000 m depth range and statistically less likely to be collected in the 0–200 m depth range than they were in the south in each of those depth ranges. Within the other depth ranges the ratio between sampling effort and successful catches was not significantly different either side of the ACC or there was insufficient data to test for significance.

Collection depths of individual species were plotted in 100 metre depth intervals to establish as accurate depth range as possible for each species. For some species (*P. antarctica, P. ambigua, P. mimas, P. mimas* and *P. delicatula*), insufficient records were available to establish confident depth ranges but in general those species south of the ACC had overlapping depth ranges, except for *P. millerae* which appears to be a deep water (>800 m) species only (Table 4.4). Of those species found north of the ACC, *P. tasmani* and *P. niwa* were found from a large range of depths (400–1800 m) but *P. chatham* and *P. erymna* were more restricted, found only between 800–1100 m.

Table 4.4. Depth distributions of *Primnoisis* species graded into 100 m depth intervals. The colours of clades match the colours marking distributions in the maps above.



Depth Intervals (m)	North of ACC								South of ACC					
	ambigua	*antarctica*	*chatham*	*erymna*	*mimas*	*niwa*	*rigida*	*tasmani*	*cf.antarctica*	*delicatula*	*formosa*	*fragilis*	*gracilis*	*millerae*
0-100	■									■				
100-200		■			■				■	■	■	■	■	
200-300									■		■	■	■	
300-400									■			■	■	
400-500						■		■	■		■	■	■	
500-600						■					■	■	■	
600-700								■			■	■	■	
700-800						■			■			■		
800-900				■				■				■	■	■
900-1000			■	■		■		■						■
1000-1100			■	■		■		■						
1100-1200							■	■						
1200-1300						■		■						■
1300-1400								■						■
1400-1500								■						■
1500-1600														■
1600-1700								■						
1700-1800						■		■						
1800-1900														

4.4 Discussion

The genus *Primnoisis* is confirmed to occur around the Antarctic continent and in southern regions of Australia, New Zealand, South America and many subantarctic islands. Many historical records were found to be incorrect so the understood distributions of existing species were often inaccurate, for example, the assumption that *P. antarctica* has a circumpolar distribution. However, three species (*P. fragilis, P. gracilis* and *P. formosa*) appear to be well-distributed around the Antarctic continent, and others have potential to be, with a couple of widely separated records. Those species collected north of the ACC have limited distributions, each restricted to isolated areas of seamounts, ridges or plateaus. However, these results are tempered by the reality of deep-sea collections—small sample sizes, large un-sampled areas and inconsistent collection success especially in hard substrate areas which octocorals prefer. The geographical and molecular positions suggest the genus may have diverged from an original population in the temperate seamounts south of Australia and spread to the subantarctic islands and New Zealand, and to the Antarctic continent, probably before or during the establishment of the ACC. Species north of the ACC were found, on average, at deeper sites than those on the Antarctic continental shelf and depth stratification of species was evident on the Antarctic continent for *P. millerae,* which was only recorded at depths below 800 m. Preliminary population observations on *P. fragilis,* with an apparent circumpolar distribution, suggest there is limited connectivity between populations on the Scotia Arc and those from east Antarctica with no shared haplotypes. However, the populations from Scotia Arc and the Ross Sea do share a haplotype, which may indicate some connectivity, a possible ancient connection or insufficient variability in the gene regions to highlight inter-population differences.

4.4.1 Allopatric speciation north of the ACC

Biogeographic conclusions inform and empower conservation decisions within our oceans and evidence to suggest some of these octocoral species are restricted to isolated areas has broad implications. Octocorals form a significant part of the benthic fauna of seamounts and continental shelf features (Sánchez & Rowden 2006) and provide important habitat associations with many other fauna (Cho & Shank 2010; Quattrini et al. 2012) but are susceptible to substantial anthropogenic impacts such as trawling and ocean acidification (Althaus et al. 2009; Waller, Watling, Auster, & Shank 2007; A. Williams et al. 2010) so the need to accurately understand species distributions and connectivity is urgent. Seamounts have traditionally been considered isolated communities with high degrees of endemism (Castelin et al. 2010; Richer de Forges et al. 2000) but there is recent acknowledgement that the situation is more complex, with studies of seamounts often limited by sample size, good control sites and generalisations not supported by all taxa or on all seamounts (Clark et al. 2010; O'Hara 2007; Rowden, Dower, Schlacher, Consalvey, & Clark 2010;

Shank 2010). Further studies have demonstrated significant connectivity between seamounts and surrounding areas in some taxa (Ameziane & Roux 2011; Miller et al. 2010; Smith et al. 2004; Thoma et al. 2009) with depth stratification possibly more significant than previously thought (Baco & Cairns 2012; Miller et al. 2011). Using five mitochondrial markers combined, Baco & Cairns (2012) examined patterns of distributions of *Narella* species at relatively short (100 kms) and long (3000 kms) distances. They found an example where a haplotype was shared between sites 3000 kms apart but was not detected on much closer seamounts, and other examples where haplotypes were restricted to single seamounts. Additionally, even with the combination of five mitochondrial markers, only 10 of the 12 morphologically-defined *Narella* species were fully resolved. They declare the current mitochondrial markers cannot reliably resolve 100% of species and thus cannot address intraspecific differences and connectivity between conspecific populations. The overall conclusion was that using these mitochondrial markers “we may not have the power to even test the hypothesis of seamount isolation….let alone refute it” (Baco & Cairns 2012). The distributions found here for the *Primnoisis* species north of the ACC do not suggest there is endemism at a small scale (individual seamounts) or at small to medium depth intervals but they do indicate endemism at the scale of general geographic features such as a group of seamounts (*P. chatham*), an oceanic ridge (*P. niwa*) or a plateau (*P.* cf. *antarctica*). This however, is not absolute with *P. erymna* found both on the Macquarie Ridge and Chatham Rise and *P. tasmani* found on multiple adjacent seamount groups and the Tasmanian shelf. These conclusions are also restricted by low levels of genetic variability in the two mitochondrial gene regions so if cryptic species, endemic to smaller geographic areas, were present they may not have been detected (Baco & Cairns 2012). Nevertheless, species specific to the geographically separated general areas suggest a lack of genetic exchange between these populations and that communities unique to those areas need protection.

4.4.2 ‘Circumpolar’ distributions south of the ACC

Species found south of the ACC were generally widely distributed although full circumpolar distributions remain largely unconfirmed due to sampling gaps. Other caveats to this conclusion are the low number of specimens examined outside the Ross Sea to Prydz Bay area (eastern Antarctica) and the recognised low level of genetic divergence in the mitochondrial gene regions of octocorals (McFadden et al. 2011). If these species brood their larvae as assumed, these wide-spread distributions would be unexpected given their presumed limited dispersal ability. Relatively well-known taxa such as the crinoid *Promachocrinus kerguelensis* (Wilson et al. 2007), the pycnogonid *Colossendeis megalonyx* (Krabbe et al. 2010) or the seastar genus *Odontaster* (Janosik & Halanych 2010) have more recently been shown to consist of cryptic species complexes, often with geographically restricted distributions. However, not all species have limited distributions. For example, “clade p3” within the species complex of *Eusirus perdentatus*in was found at five locations around the Antarctic continent (Baird et al. 2011) and Allcock et al. (2011) similarly found the octopus *Pareledonea equipapillae* to have a circumpolar distribution. Arango et al. (2011), although describing significant genetic differentiation between geographically isolated populations of the ‘circumpolar’ pycnogonid *Nymphon australe*, interpreted this as limited contemporary genetic flow between populations of a single species which had long ago colonised available habitats during different geological conditions. Thus small-scale population structure can be entwined with large-scale distributions with identical haplotypes found across vast distances around Antarctica even for organisms with seemingly limited dispersal capabilities. *Primnoisis fragilis* was found to share a haplotype between the Scotia Arc, the Ross Sea and Commonwealth Bay indicating an extensive distribution, however, it is likely that these two mitochondrial gene regions are insufficiently variable to detect fine scale intraspecific variability or population differences (Baco & Cairns 2012; McFadden et al. 2011). Moreover, the recognised slow rate of mitochondrial variation in octocorals may mean shared haplotypes are reflective of ancient connections and ancestors and are not necessarily indicative of any contemporary gene flow. Similar to recent studies on other taxa, *P. fragilis* could be considered circumpolar but may lack full genetic connectivity and could not be considered a single, panmictic population (Arango et al. 2011; Wilson et al. 2007). However, future research on more variable markers such as microsatellites would be necessary to fully determine the extent of the connectivity or isolation of these populations (Wang 2011). In deep-sea scleractinian corals, microsatellite data was found to demonstrate structuring between conspecific populations when mitochondrial data did not (K. Miller pers. comm.).

Interestingly, Gutt & Piepenburg (2003) found *Primnoisis* colonies to be one of the first colonisers after iceberg scour which would suggest fast growth and good dispersal capabilities. This may explain the extensive distributions for the *Primnoisis* species south of the ACC with opportunistic habitat colonisation around the continent (Thatje et al. 2005). However, *Primnoisis* species are thought to be brooders with low dispersal capabilities, and this combined with fast colonisation of recently ice-free habitat followed by multiple isolation events caused by glacial cycles would be expected to facilitate diversification and allopatric speciation (Allcock & Strugnell 2012; Rogers 2007; Wilson et al. 2009). Nevertheless, only five species of *Primnoisis* were found across all Antarctic continental samples and over a hundred years of research. The expansion and secondary connection of these early colonising and fast-growing populations during interglacial periods could have led to genetic mixing and cross-fertilisation, obscuring any speciation, especially if the assumption on reproductive method is incorrect and it is actually a broadcast spawner.

Alternatively, the colonisers may have been from well-mixed populations surviving in deep-sea refugia (Thatje et al. 2005) although the *Primnoisis* species with the widest distributions were not found in the deeper samples and there appears to be depth stratification of the species. It also must be considered that octocorals are known to have extremely low levels of genetic variability in the mitochondrial gene regions and traditional morphological characteristics are subjective and plastic even within colonies, so cryptic or unrecognised species and/or intraspecific genetic differentiation may be present but remain undetected.

4.4.3 Possible origins of *Primnoisis*

Phylogenetic estimations combined with geological history suggest south eastern Australia as a possible origin of the genus *Primnoisis.* The final Gondwanan link between Australia and Antarctica was bisected by powerful westerly currents south of Tasmania approximately 34 Ma as Australia moved north (Carter, McCave, & Carter 2004) and would have effectively separated populations on the two continental shelves. Furthermore, other water masses such as the Subantarctic Front and the Subtropical Front flowed across the Tasmanian continental shelf and around and across the continental plateau south and east of New Zealand (Fig. 4.10).

These vicariant populations then diverged into the *P. tasmani* lineage and an ancestor of the other *Primnoisis* species. Presumably this ancestor diverged again, forming the two subgenera lineages. The currents are likely to have aided distribution of both subgenera from south of Tasmania to the Macquarie Ridge and north to the Chatham Plateau and to the Antarctic continental shelf as the landmasses separated (Fig. 4.8). Eventually the ACC was fully established after the opening of the Drake Passage at the Antarctic Peninsula, approximately 28–20 Ma, and the southern populations on the Antarctic continental shelf were isolated from those north. Thus it is suggested both subgenera were present north and south of the ACC, and since then speciation and divergence within the subgenera has been isolated either side of the current. Most of the species south of the ACC may have speciated in sympatry and spread around the continent while those occurring north of the ACC likely speciated in allopatry and formed isolated species, endemic to generalised topographic features.

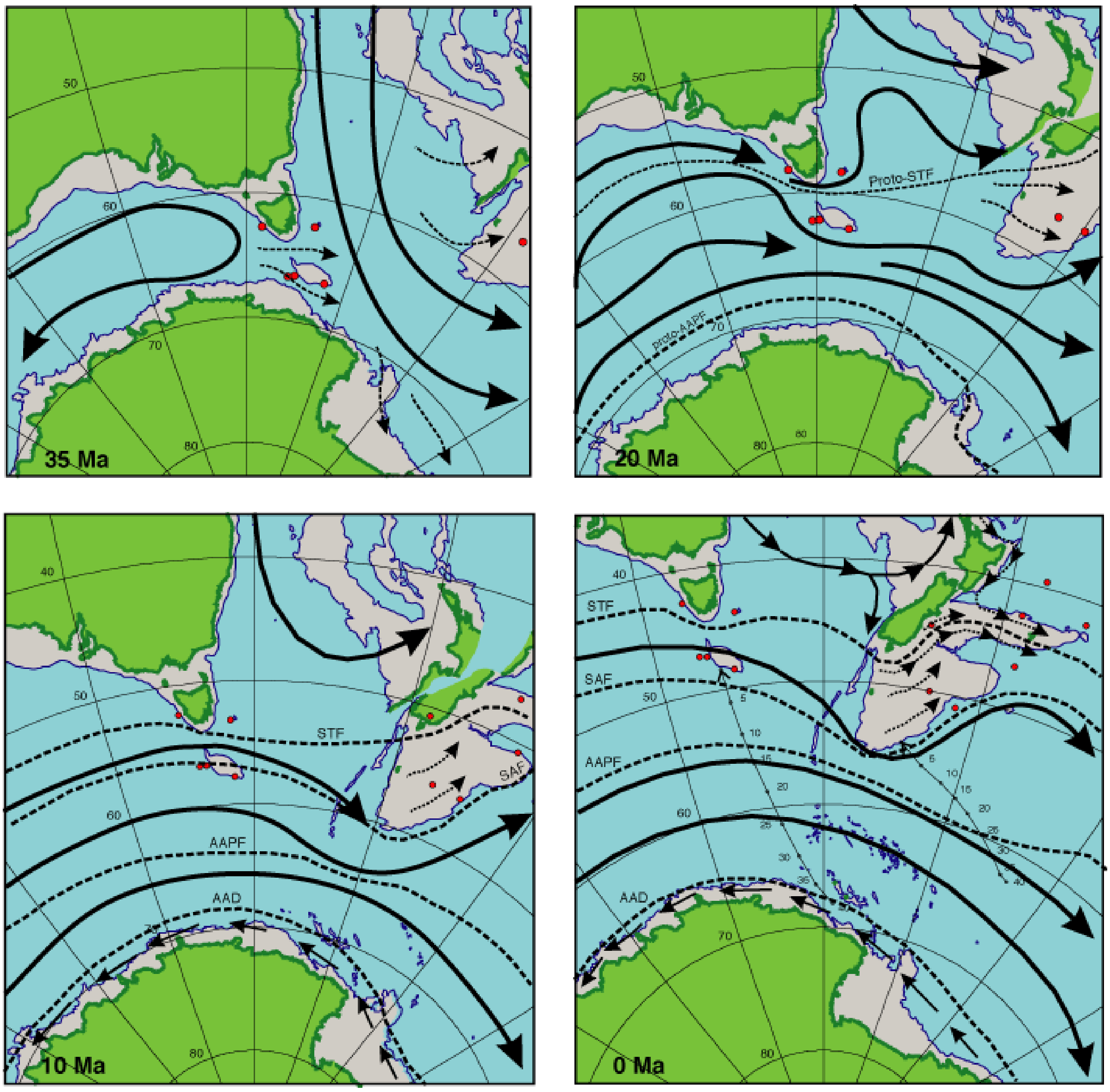


Figure 4.10. from Carter et al (2004) Reconstructed frontal systems and ocean surface circulation for the Australasian Southern Ocean at 35, 20, 10, and 0 Ma. Base map tectonic reconstruction by Sutherland (after Cande et al. 1995; Sutherland 1995; Royer and Rollet 1997). STF = Subtropical Front, AAPF = Antarctic Polar Front, AAD = Antarctic Divergence, SAF = Subantarctic Front. Red points represent sites drilled for Carter et al. (2004).

A notable complication stems from the position of the deep-sea species *P. millerae* (south of the ACC) as basal to other species of *Delicatisis* including particularly *P. niwa*, present only on Macquarie Island which is north of the ACC. The *Delicatisis* ancestor may have been initially restricted to south of the ACC, but colonised Macquarie Ridge at some stage, for example during glacial periods when the production of northward flowing Antarctic bottom water is strongest (Brandt 2005), or during a period when the ACC was positioned further north (Barnes, Hodgson, et al. 2006). Notably the *Primnoisis* subgenus appears to have very little diversification, north or south of the ACC—this may be a factor of the gene regions used.

P. tasmani was isolated on the Australian continental shelf and despite significant molecular divergence from the other *Primnoisis* species, remains morphologically similar to those in the *Delicatisis* subgenus, due perhaps to a lack of selective pressures on morphology. Potential ancestral links between *P. tasmani* and other remnant Gondwana populations of *Primnoisis* in South Africa and South America would be an interesting future research question.

Specimens of a closely related genus *Notisis,* were included in the phylogenetic reconstruction and appear to have diverged from the *Delicatisis* lineage on the Antarctic continental shelf. *Notisis* is restricted to Antarctic waters and has been recorded at numerous sites including the Antarctic Peninsula, West Young Island (Alderslade 1998), Commonwealth Bay, and Scotia Arc (data not included) so also appears to be very widely distributed. It has not been recorded north of the ACC.

There are very few octocorals present in the fossil record world-wide and Antarctic fossils in general are particularly rare, damaged by glaciation or unsuitable for dating (Allcock & Strugnell 2012). Additionally, many difficulties such as accurate estimates of evolutionary rates still forestall confident dating of divergence events. As such, there was little opportunity to apply an accurate molecular clock to these divergences but obviously this would greatly enhance possible ancestral scenarios. A few internodes from the lower Miocene, found in southern New Zealand, were assigned to *Primnoisis ambigua* by Grant (1976). Given the uncertainty around the taxonomy of *P. ambigua*, the known distribution (Kerguelen Island) and the inconsistency of other *Primnoisis* identifications by Grant in the same paper (Chapter 3), this assignation is unlikely to be correct and the placement in the genus remains uncertain.

4.4.4 Depth

There is some indication of depth structuring in the distribution of species recorded south of the ACC. In general, *Primnoisis* specimens were found in greater numbers per unit effort in deeper waters north of the ACC while occurring more commonly in the shallower waters south of the ACC. This suggests a possible temperature constraint to the genus with distribution north of the ACC limited to the deeper, cooler waters. At a species level, *P. millerae* was only recorded at depths of over 850 m, with an average collection depth of over 1000 m and was absent from the relatively extensively sampled shallower depths. This depth stratification corresponds with the approximate delineation between the continental shelf and the continental slope (Brandt, De Broyer, et al. 2007) and indicate *P. millerae* is likely part of the upper-slope fauna. All other species collected south of the ACC were found at shallower depths (100–900 m) and are likely isolated by depth from *P. millerae* but otherwise occur in sympatry. Soler-Membrives et al. (2009) also found a bathymetric distinction in faunal composition of pycnogonid samples taken from the shelf (“from the shallows up to 900 m") and those collected from deeper water (>900 m), and Barnes & Kuklinski (2010) found Antarctic bryozoans formed distinct shelf, slope and abyssal faunas with support for only minimal connectivity between these depth-stratified populations. Indeed, they suggest it is unlikely the deep-sea fauna recolonised the shelf area after glacial periods because they would have to migrate against the downwelling, northward flowing Antarctic Deep Water.

North of the ACC, only *P. tasmani* and *P. niwa* were recorded in sufficient numbers to give a good indication of a bathymetric range. In both cases they were found from 400–1800 m although admittedly trawls outside this range were limited. Thresher et al. (2014) found strong depth stratification on the seamounts where the majority of *P. tasmani* specimens were collected including a faunally unique zone below 2000 m. This species straddles the shallowest of their three zones which are characterised by diverse communities including many octocorals, and live and dead *Solenosmilia* reef, and did not extend into the deeper zones. The nearby Australian continental shelf has massive areas of suitable depth habitat and indeed *P. tasmani* was found at ~600 m and ~1700 m on the eastern Tasmanian coast and ~1000 m on the southern Victorian coast indicating it is not endemic to the seamount group and may occur in this depth range around the south eastern Australian coastline. As Howell et al. (2010) found, the faunal composition of the seamounts may largely correspond with that of the nearby continental shelf, although biomass may differ (Rowden, Schlacher, et al. 2010).

Both *P. niwa* and *P. tasmani* occur deeper on average than *Primnoisis* species in the waters south of the ACC, suggesting a cool temperature influence on their distribution, which corresponds with O'Hara & Tittensor (2010) who found temperature was the most important environmental predictor of ophiuroid distribution on seamounts.

4.4.5 Summary

These results indicate different geographical and evolutionary patterns for *Primnoisis* species north and south of the ACC. Those species situated north of the current appear to lack effective genetic connectivity (i.e. are endemic) at a regional scale while those species south of the ACC have extensive distributions around the Antarctic continental shelf, with some indication of faunal distinction by depth. There was little evidence of finer-scale population structuring either within geographic regions or within species but this may be due to insufficient variability in the genetic markers. The lack of fossil evidence of octocorals makes hypothesising on evolutionary events problematic, however a molecular reconstruction of ancestral relationships suggests southern Australia as a possible origin of the genus with probably vicariant speciation at the separation of the

Australian and Antarctic continents and further diversification around the Antarctic continent and available habitat north of the ACC.

The ability to accurately understand and predict distributions and connectivity of marine biota is critical in the endeavour to protect and maintain biodiversity in our oceans. Critical to that is the ability to accurately and consistently delineate species boundaries and identify possible cryptic or unrecognised species. Combining multiple lines of evidence such as morphological and molecular synergies is becoming increasingly common and effective, although there remains debate on which are the most useful gene regions, type of analyses and approaches when morphological, mitochondrial and nuclear analyses differ (Rogers 2007). A far greater understanding of the octocoral genome is quickly developing (Brockman & McFadden 2012; Brugler & France 2008; Figueroa & Baco 2014; Herrera et al. 2010; Pante et al. 2013; Uda et al. 2013) including the utility of single nucleotide polypmorphisms (McFadden et al. 2011) and microsatellites (Porto-Hannes & Lasker 2013; Smilansky & Lasker 2014) and future molecular research will hopefully inform and strengthen our understanding of species distributions. Molecular tools are also useful to predict connectivity and reconstruct ancestral lineages and have the potential to significantly alter our understanding of species boundaries, deep-sea distributions and the historical and contemporary processes driving those distributions—all necessary for effective conservation of the largely undescribed diversity present in the Antarctic marine fauna.

Chapter 5. General Discussion.

Deep-sea octocorals of the genera *Anthothela* and *Primnoisis* are a diverse and ecologically important part of the Southern Ocean fauna. The taxonomic revisions undertaken here have illuminated the inaccuracies and inadequacies present in much of the existing taxonomic literature on these two genera, and with 10 new species and 2 new genera described, the thesis illustrates that there was significant unrecognised biodiversity within these genera and highlights the possibility that many other octocoral genera harbour the same level of hidden diversity. Using a combination of morphological characters and molecular phylogenies, it was found that specimens originally thought to be 6 species of *Anthothela* actually comprised 4 genera (*Anthothela, Victorgorgia, Lateothela* n. gen. and *Williamsius* n. gen.) and 14 species, 5 of which are newly described (Chapter 2). The revision of the genus *Primnoisis* (Chapter 3) was able to examine the morphological boundaries of the genus, and essentially confirm the working morphological definition (Alderslade 1998) although the phylogeny remains unresolved. The revision recognised 7 of the original 8 species within the genus and described 5 additional ones. Overall the results achieved have significantly clarified the delineation of the two genera and species within. In addition, biogeographic patterns have revealed the importance of the Antarctic Circumpolar Current (ACC) in the isolation of subantarctic and Antarctic deep-sea fauna and this has clearly had an important influence on speciation processes within *Primnoisis* (Chapter 4). The unexpected finding that the genus likely has its origins in temperate Australian waters and is not of Antarctic origin as previously assumed, will also have implications for future studies on the evolution of Antarctic marine fauna. Together these results contribute to a global effort to improve octocoral systematics and to understand faunal connections within the deep-sea.

5.1 Deep-sea octocoral taxonomy and the effectiveness of a multidisciplinary approach

In general, taxonomic studies of deep-sea taxa are constrained by a lack of basic ecological information such as reproductive traits, niche habitat selection, prey interactions, and even in situ colour (Janosik & Halanych 2010), all of which can be important characteristics to aid taxonomic decisions in terrestrial or shallow water species. Currently, the most effective approach for strengthening taxonomic decisions in deep-sea taxa is the combination of morphological and molecular phylogenies in the hope that each can inform and empower the other. In deep-sea octocorals, taxonomy has been poorly understood and haphazardly studied, limited by accessibility and the low frequency of collection, and is often made more difficult by the inadequacy of the morphological characteristics and the poor quality of much of the published literature. Fortunately the situation has been improving significantly with substantial effort engaged in taxonomic revisions and the descriptions of new taxa (e.g. Alderslade & McFadden 2012; Taylor et al. 2013; Zapata-Guardiola, López-González, & Gili 2012), the beginnings of familial and generic rearrangements and redefinitions which correspond to monophyletic groups (e.g. McFadden & van Ofwegen 2012c; McFadden & van Ofwegen 2013), and the mapping of small- and large-scale distributions and geographic or bathymetric influences (e.g. Baco & Cairns 2012; Herrera et al. 2012; Pante et al. 2012). Most of these recent studies, including this thesis, often found historical designations and assumptions are inaccurate or ambiguous, and have commonly revealed previously unrecognised diversity and complex molecular relationships which indicate many existing taxonomic groups are polyphyletic. Importantly, most of these recent studies have employed a combination of morphological and molecular evidence to arrive at taxonomic classifications which are more robust and repeatable than those based on just one method in isolation. For example, in McFadden & van Ofwegen (2013) specimens nominally from the two genera *Eleutherobia* and *Alcyonium* were found to fall outside the large Holaxonia-Alcyoniina clade in a molecular phylogeny and were subsequently found to have morphological differences that corroborated the genetic evidence of speciation such as unusual spherical sclerites, among other characteristics. Thus this group, which was subsequently described as a new family and genus, is now detectable with molecular analysis or morphological assessment, and retrospective morphological assessments of historical specimens or descriptions may prove to uncover further specimens from the new family. Other recent examples have found traditional morphological characteristics that align with genetic clades (e.g. Breedy et al. 2012; McFadden & van Ofwegen 2012a, 2012c; McFadden, van Ofwegen, Beckman, Benayahu, & Alderslade 2009; Vargas, Eitel, Breedy, & Schierwater 2010), and in another example, the decision to synonymise most of the existing genera within the Melithaeidae was made based on the combined absence of strongly defined clades or morphological differences (Reijnen et al. 2013)

Morphological characteristics of *Anthothela*, *Victorgorgia* and *Lateothela* n. gen. were found to consistently correspond with molecular clades and all three genera are now identifiable with both lines of evidence (Chapter 2). Morphological features included historically recognised characteristics like growth form, the presence and positions of coelenteric canals, the type of sclerites dominant in the cortex, but crucially also include characters largely overlooked or considered of no value, specifically the form and arrangement of sclerites in the tentacle rachis and the pinnules. *Anthothela* was found to have long, spatulate clubs in the tentacles, *Victorgorgia* has a newly defined sclerite, the josephinae club, and *Lateothela* n. gen. has spiky versions of josephinae clubs. Historically, although tentacle sclerites are part of the armoury of polyps, it was common for just those of the polyp body to receive attention. Alderslade & Shirwaiker (1991) were the first to show polyp sclerites could be used as a character in *Sinularia*, *Sarcophyton* and *Lobophytum* and more recently McFadden et al. (2006) and (2009) established clearly that the occurrence and form of the sclerites in the polyps, particularly in the tentacles, reflected phylogenetic clades within the genera. More recently, Alderslade (pers. com.) has found tentacle sclerites to vary among species nominally assumed to be *Cornulariella* indicating the probable existence of different genera. In gorgonians, polyp sclerites have been considered important for a long time, but these were mostly only body sclerites and the nature of the tentacle sclerites in many genera and species have rarely, if ever, been recorded. However, tentacle sclerites were extensively recorded by Alderslade (1998) in his monograph on some groups of Isididae, where it was shown that, although all tentacle rachis sclerites were of the basic crescent form and pinnule sclerites were absent across all genera, the arrangement and nature of the sclerites in the anthopoma was very informative taxonomically. Additionally, live colour appears to be a useful distinguishing characteristic for the genus *Victorgorgia* (Chapter 2), and with the increasing ease of photography soon after collection and/or developing technologies to facilitate in situ photography, colour may prove to be an important taxonomic feature for other octocoral genera. Recently, a new genus of Isididae was described which has a number of unusual morphological characteristics not previously recorded such as a fleshy tegument and unusual sclerites (Alderslade & McFadden 2012), and a new species of *Keratoisis* has been named for an unusual nacreous lustre found on the internodes (Dueñas, Alderslade, & Sánchez 2014). Considering how many historical families and genera are believed to be polyphyletic (McFadden in Daly et al. 2007), subtle, overlooked or new morphological characters (especially those collated by retrospective examinations informed by molecular phylogenies (Knowlton 2000)) may hold a key to a wide-ranging reformation of Octocorallia systematics.

However, morphological lines of evidence do not always correspond with molecular evidence (Carstens, Pelletier, Reid, & Satler 2013) and hence this combined taxonomic approach is not always widely applicable. Particularly in cnidarians, the morphological or molecular variability at a species level is often insufficient to be reliably used for species delineation (Baco & Cairns 2012; Knowlton 2000). Currently, molecular and morphological correspondence appears to be unambiguous only at a genus level (or higher) for octocorals and even then this is not consistent across genera. For example, in Chapter 3 some specimens of *Primnoisis* divided into two well supported clades, but the morphological traits associated with these groups (such as the angle of the polyps and the size of the sclerites) were not comparable to morphological distinctions usually used to distinguish other Mopseinae genera (Alderslade 1988) and thus the clades were recognised only as new subgenera, *P.* (*Primnoisis*) and *P.* (*Delicatisis*). Similarly, a deep division within the *Primnoisis* molecular phylogeny separating *P. tasmani* n. sp. from the other *Primnoisis* species could be indicative of a genus level division but is not reflected in the morphology. For that reason this species is placed in *Primnoisis* with morphological stasis a possibility (Rocha-Olivares, Fleeger, & Foltz 2001). In a contrasting decision, McFadden & van Ofwegen et al. (2012c) described three sister species which differ morphologically but are very similar genetically. They explicitly state "The species included in *Inconstantia*, gen. nov., display a remarkable diversity of colony growth forms and sclerite types that would normally preclude assigning them to the same genus" (McFadden & van Ofwegen 2012c). In this case, the authors give greater weight to the molecular evidence than to the traditional morphological characteristics.

How to weight evidence when molecular results are not well reflected morphologically, and vice versa, presents a new and ongoing difficultly in taxonomic studies. Ideally species delimitation should be informed by as many lines of evidence as possible (e.g. molecular, morphology, life history, geographical distribution and behaviour) and when there is incongruence any decisions should be explained explicitly (Carstens et al. 2013; Damm, Schierwater, & Hadrys 2010). Carstens et al. (2013) also suggest decisions on species delimitation should be conservative—if there is incongruence they argue for caution to guard against proposing false evolutionary lineages. However, for deep-sea samples often the only other information available is geographical placement and this comes with inherent difficulties as well because for many deep-sea groups, octocorals included, so little is understood of their connectivity, dispersal ability and longevity that two widely separated samples cannot be discounted as being from the same species. In the taxonomic reviews within this thesis (Chapters 2 and 3) species decisions were based on the congruence of at least two of the three lines of evidence available; i.e. morphology, molecular or geographic. For octocorals there are the additional difficulties associated with the highly conserved nature of the mitochondrial genome, so recent speciation may not be reflected in the mitochondrial gene regions (McFadden et al. 2011), plus most morphological characteristics vary along a continuum and there are few definitive characteristics among species and hence morphological similarity is open to subjectivity. In essence this means all three lines of evidence (morphology, molecular and geography) are potentially ambiguous but also reinforces the importance and utility of a multidisciplinary approach for deep-sea octocoral in order to achieve the most robust taxonomy possible.

While coupling molecular clades with morphological synapomorphies may sometimes greatly strengthen species delineations, most current molecular analyses still only include recently collected samples (due to age effects on sequencing success) and only use a small percentage of a genome. Molecular methods are improving rapidly and next-generation sequencing will greatly expand the percentage of the genome available (Reitzel et al. 2013). However while we continue to use the traditional taxonomic structure with existing binomials linked to particular type specimens, there still exists the difficulty of assigning a current species name to a genetic lineage. In the majority of cases the type specimens are either unavailable or are too old for successful genetic extraction, and assignations have to be based solely on morphological evidence. This situation can only be alleviated by assigning fresh material that is essentially morphologically and geographically identical to each type in question, a difficult if not impossible task for deep water organisms (both in practical and financial terms), or developing molecular technology so that old type specimens can be sequenced. Alternatively, the scientific world could establish an entirely new nomenclature system which is based on genetic lineages only (molecular types) and existing binomials are abandoned, although this approach has limited support (Knapp, Lamas, Lughadha, & Novarino 2004). Any link with the fossil record, and hence estimations of evolutionary age, rates of divergence and ancestral systematics would be lost and the massive legacy of natural history collections would become redundant (Wiens 2004; Will & Rubinoff 2004). Staying within the traditional structure, this thesis has proposed the coupling of existing genus and species names with genetic lineages for *Anthothela grandiflora,* the genus *Victorgorgia, Primnoisis fragilis, P. delicatula, P. gracilis* and *P. formosa*. These are based on an informed understanding of morphological variability present within each group and will serve as a reliable template for future genetic comparisons.

Although there are limitations with all approaches, this thesis along with other recently published work has shown that more robust taxonomic decisions can be reached by using a combined approach and thus the future of octocoral taxonomy, as well as many other marine invertebrate groups, likely rests in a multi-disciplinary approach.

5.2 Delineation of species and the utility of character-based genetic analysis

Octocorals are known to have a highly conserved mitochondrial genome, possibly as a consequence of a mismatch repair gene exclusive to octocorals (Bilewitch & Degnan 2011; McFadden et al. 2011). This gene (mtMutS) is, paradoxically, the most phylogenetically informative mitochondrial gene region examined to date. It is frequently used in systematic studies of octocorals but the mtMutS gene, along with many other mitochondrial gene regions within octocorals, can be invariant even between corals that are separated by vast geographic distances. Untangling whether such patterns reflect true global distributions and high levels of connectivity within deep-sea taxa, or simply reflects the lack of variability in the gene region is difficult and confounds accurate taxonomy (e.g. Baco & Cairns 2012; Herrera et al. 2010; Smith et al. 2004). Within octocoral taxonomists there is a general agreement that these commonly used mitochondrial gene regions are “imperfect” for a species-specific genetic marker (e.g. a barcode) (McFadden et al. 2011), especially as there is no clear gap between intra and interspecific genetic distances. In the taxonomic revisions in this thesis (Chapters 2 and 3), species-level variation within the genera or sub-genera was very low, often represented by only a few differing nucleotides within the chosen gene regions. In Chapter 2, *Anthothela grandiflora* and *A. vickersi* were found to share haplotypes but had widely separated geographic distributions (northern Atlantic cf. southern Australia/New Zealand) and different sclerite forms, thus here they are kept as separate species with a greater weight placed on morphological and geographic criteria than on molecular data. Herrera et al. (2012) came to a different conclusion for the deep-sea octocoral species *Paragoria arborea* which also shares haplotypes across the northern Atlantic and southern ocean with the authors concluding it as a single well-distributed species with only minor morphological differences and an intraspecific genetic distance below 1%. A review by Knowlton (2000) of how genetic analysis may influence species recognition in marine taxa indicated similar sorts of discrepancies among related species in many taxa. For example, even in the relatively well studied molluscan fauna she calls the complexity of results “sobering”, with disparity between molecular and morphological data both in sympatric and allopatric populations, and evidence of a variety of hybridization patterns and differing results dependent on methods employed (Knowlton 2000and references within). Many crustacean taxa have been shown to harbour cryptic species (or genetic clustering which has been undetected morphologically) on both large and small scales (Baird et al. 2011; Lörz, Maas, Linse, & Coleman 2009) but others have not (Raupach et al. 2010). It is clear there is no consistent solution or approach to species delimitation even between related taxa and this is perhaps to be expected given speciation is a gradual process with a great variety of drivers. Different interpretations of subjective measures like phenotypic dissimilarity and measures like genetic distance which are difficult to compare across taxa groups are not unusual (Carstens et al. 2013) but each situation is different and, if decisions are explicitly explained, can still inform and enhance future taxonomic endeavours.

In this thesis, species level differences were often subtle, complicated by the fact that many species are represented by singletons (only one specimen), a common problem in deep-sea biodiversity studies (Vrijenhoek 2009). Within *Victorgorgia* for example, *V. josephinae, V. argentea, V. macrocalyx, V. alba* and *V. nyahae* are all described on one or two specimens. Additionally, the *V. argentea, V. macrocalyx* and *V. alba* type specimens were collected in 1891, 1899, and 1902 respectively with no or few confirmed specimens collected since. In Chapter 3 *Primnoisis antarctica, P. rigida, P. ambigua, P. delicatula* and *P. mimas* are all defined on one or two, often old, specimens. Thus in these cases there were little or no opportunities to establish intraspecific morphological or molecular variability. Indeed, the sequences obtained from the subgenus *P.* (*Primnoisis*) were almost invariant across vast distances. *P. fragilis* specimens from Scotia Arc, the Ross Sea and the

Shackleton Iceshelf differed by only a few nucleotides and these haplotypes differed by an additional two nucleotides from the single haplotype shared by *P. erymna* and *P. chatham* from Macquarie Ridge and Chatham Rise. Thus the three species in the subgenus, separated by enormous distances including across the ACC, had genetic distances analogous to intraspecific variation (McFadden et al. 2011). This subgenus appears to have less variability at these gene regions than the subgenus *P.* (*Delicatisis*) which had differences of 12 nucleotides and a short microsatellite region across five species (Chapter 3). This raises the possibility that closely related taxa have different rates of evolution in a particular gene region. McFadden et al. (2011) found that deep-sea Calcaxonia taxa demonstrated significantly less (10 x for COI and 2–4 x for mtMutS) intra-and inter-specific variability in the two mitochondrial gene regions than that found for species and genera within the Holaxonia-Alcyoniina clade. These two studies are not immediately comparable as the findings are at significantly different hierarchical levels (suborders cf. subgenera), but nevertheless different evolutionary rates between taxa (even closely related taxa) seems possible and should be considered during marker selection. For understudied fauna like octocorals, this is almost impossible to know in advance, but new molecular techniques which facilitate use of a much greater spread of a genome should help to average out these evolutionary disparities. –

In the case of low genetic variability, a character-based approach (or haplotype comparisons), included in both Chapter 2 and 3, may be more effective at delimiting species than genetic distances (Baco & Cairns 2012; Damm et al. 2010; McFadden et al. 2011; Rach et al. 2008; Thoma et al. 2009). Here, just a few base pair differences were found between some species (for example the *A. grandiflora/A. vickersi* haplotype differed from the *A. aldersladei* n. sp. haplotype by a single base pair yet corresponded to obvious morphological distinctions), but small differences such as these in highly conserved gene regions can be important. There is increasing recognition of the potential of single nucleotide polymorphisms (SNPs) for phylogenetic research—they are numerous and widespread in any particular genome, occurring in neutral regions and markers under selection, are well represented by relatively simple mutational models, and do not require large DNA fragments to be sequenced thus facilitating the use of degraded DNA (Morin, Luikart, Wayne, & group 2004; Reitzel et al. 2013). One of the difficulties originally associated with SNPs, that of the cost and potential bias of ascertainment of a large number of SNPs in non-model organisms, has been largely overcome due to high-throughput sequencing techniques (Reitzel et al. 2013). Thus a large percentage of a genome can be sequenced in a time effective manner without bias from pre-existing knowledge of gene regions, plus a significant number of individuals can be sequenced during SNP discovery to ensure a representative example of SNP variability (Brumfield, Beerli, Nickerson, & Edwards 2003; Reitzel et al. 2013). Indeed, large sample sizes in a taxonomic study using SNPs are crucial as confidence in the accuracy and relative frequency of each particular haplotype increases with each additional specimen (Damm et al. 2010; McFadden et al. 2011; Morin et al. 2004). The haplotype comparisons conducted here were hampered by a small number of specimens and a relatively small number of SNPs but continuing research on these gene regions and others will help to build the large sample sizes necessary to reliably interpret SNPs.

5.3 The biogeography and possible origin of *Primnoisis*

The combination of the taxonomic revision of *Primnoisis* (Chapter 3) with all confirmed sampling localities generated a robust and current distribution for the genus and species within (Chapter 4). The genus is confirmed as circumpolar and relatively common in deep temperate waters north to 37°S, which expands the known distribution of the genus as it has traditionally been assumed to be almost exclusively Antarctic and subantarctic (Alderslade 1998; Bayer & Stefani 1987b). Those species recorded north of the ACC were found to be endemic to regions (seamount groups, ridges, plateaus) while those south of the ACC were found to have much wider distributions around the Antarctic continental shelf including three species with likely circumpolar distributions (*P. fragilis, P. formosa, P. gracilis*). This contemporary disjunction of species found north and south of the ACC accords with that found in other benthic marine invertebrate taxa such as pycnogonids (Griffiths et al. 2011) and holothurians (O'Loughlin et al. 2013). Interestingly, both these studies were investigating multiple genera and species and both found the same pattern of localised endemic species north of the ACC and relatively broad distributions in species occurring south of the ACC. Clearly the ACC is an important evolutionary force causing separation between Antarctic and subantarctic benthic fauna and influencing speciation processes across a wide range of taxa, and future changes in the position and strength of the ACC could be expected to impact on the associated fauna. The fauna found below ~100 m on the Antarctic shelf are in very thermally stable, cold waters and appear to have a low tolerance to rapid temperature fluctuations (Barnes, Peck, & Morley 2010; Clarke, Murphy, et al. 2007). Thus rapid temperatures changes such as would be experienced crossing the ACC or if the ACC moved further south could be expected to adversely impact this fauna, although Barnes et al. (2006) suggested that long-term survival of biota of occasional incursions of warmer water from the upper ACC onto the Antarctic shelf indicates these taxa may have a wider temperature tolerance than previously expected. Some of taxa found north of the ACC, especially near the Antarctic Peninsula, are already experiencing rapid warming (Clarke, Murphy, et al. 2007) but their ability to migrate further south to cooler waters would be inhibited by the strong flow of the current. A complex matrix of bathymetric and thermal tolerances, dispersal mode and suitable habitat availability is likely to influence the colonization success of these organisms moving south into Antarctic waters (Clarke, Murphy, et al. 2007). However, given that most of the *Primnoisis* species (Chapter 4) and holothurians lineages (O'Loughlin et al. 2013) found north of the ACC were restricted to particular areas, their dispersal abilities seem restricted and successful migration south as global waters warm may be unlikely. Recognition that these topographic features probably harbour multiple endemic species with little or no connectivity with other regions must inform and enhance conservation decisions for these areas.

North of the ACC, each *Primnoisis* species was found in one geographic region only, although within those regions they were recorded numerous times and sometimes spread over some distance if there was connecting habitat. For example, *P. tasmani* was recorded from seven different seamounts, the continental shelf south and east of Tasmania, as well as the southeast of Victoria. *Primnoisis erymna* was recorded on the Macquarie Ridge and the Chatham plateau (Chapter 4). The implication of these distribution patterns is that there is good connectivity within the regions but limited connectivity between them, with large oceanic distances and the absence of appropriate habitat that might serve as stepping stones to dispersal presumably inhibiting such connections. That these species are endemic to regions serves to inform management decisions and cooperative conservation polices across national and state boundaries, however the assumption that there exists good connectivity within each region must be tempered by the recognised lack of variability within the mitochondrial gene regions employed. Isolation or lack of connectivity within populations even between adjacent seamounts or over depth gradients is recognised for some taxa (Baco & Cairns 2012; Doughty et al. 2014; Miller et al. 2011) but often can only be detected with numerous or more sensitive gene markers and a relatively large number of sequenced specimens.

Those species recorded on the Antarctic continental shelf were generally found to have extensive distributions which could be explained by the massive expanse of continuous suitable habitat and the constant, strong circulation influence of the ACC assisting the spread of taxa (Chapter 4). Existing protection measures for benthic fauna around Antarctica including restrictions on fishing in Vulnerable Marine Ecosystems (CCAMLR 2013) and the establishment of some Antarctic Specially Protected Areas (ASPAs) and Antarctic Specially Managed Areas (ASMAs) (CCAMLR 2012), will ensure some protection for these benthic species especially if gene flow across large distances is ongoing. Three of the species on the Antarctic continent (*P. gracilis, P. formosa* and *P. fragilis*) were relatively common in suitable habitats, and they apparently grow quickly and have the ability to rapidly recolonise affected areas (Teixidó et al. 2004) so the protection offered in the ASPAs and ASMAs could be expected to ensure their survival. However, many nominal species on the Antarctic continent have been shown to consist of cryptic species with very limited distributions (e.g. Allcock et al. 2011; Baird et al. 2011; Krabbe et al. 2010) so the same caveat applies as above—the gene regions may not be variable enough to detect cryptic speciation or population structures and if cryptic species exist, then the lineages are unlikely to have sufficient protection from current conservation measures.

There is some structuring by depth evident in Antarctic waters, with *P. millerae* only recorded from waters deeper than 850 m while other species on the Antarctic continent were found in waters between 100–900 metres (Chapter 4). The depth stratification corresponds to the Antarctic continental slope (1000–3000 m) and shelf (<1000 m) but there were very few samples from areas off the continental shelf available so additional sampling may dilute this structuring. Similar disjunctions between shelf and slope fauna have been found in other taxa around Antarctica (Barnes & Kuklinski 2010; Soler-Membrives et al. 2009) and Brandt et al. (2007) indicated the abyssal depths (>3000 m) also have a distinct fauna for many groups. However, for octocorals the Antarctic abyssal fauna is very similar to that found in other oceans and almost exclusively consists of sea pens which prefer soft bottom habitats (Brandt, De Broyer, et al. 2007). The Antarctic deep shelf and slope octocoral fauna is generally poorly known but recent efforts have improved the situation with new descriptions of genera and species (e.g. Taylor et al. 2013; Zapata-Guardiola & López-González 2010a; Zapata-Guardiola & López-González 2012). However, these have all concentrated on one family, the Primnoidae, and almost no samples were included from >1000 m on the Antarctic continental shelf. The lack of data from the Antarctic deep slope and the discovery here of *P. millerae*, a species that appears only to exist at depths >1000m, suggest an unexplored habitat for octocorals on the Antarctic continental slope and potentially an unrecorded diversity of fauna.

The origins of the genus Primnoisis would appear to be in south-east Australia. The species *P. tasmani,* which is endemic to south east Australia, was basal to all other specimens of *Primnoisis* on a deep division, indicating an ancient divergence possibly corresponding to the separation of Gondwana and the subsequent evolution of the ACC. This is contrary to the original assumption that the genus originated in Antarctica, an assumption which was based on the location of most of the described diversity. It is also contrary to the assumed origin of many other Antarctic genera, based on the high level of endemic species found in the waters around Antarctica, suggesting a radiation from an origin 'hot-spot' (Brandt 1999; Rogers 2007). Briggs (2003) suggested that remnant temperate taxa from Gondwana went extinct as the temperature fell during the establishment of the ACC but perhaps the ancestor of *Primnoisis* evolved and adapted to the temperature changes around Antarctica into the extant fauna here recorded as common and endemic to Antarctica. After the establishment of the ACC, there appears to be little evidence of recolonisation of the Antarctic continental shelf from temperate species moving south (Fraser, Nikula, Ruzzante, & Waters 2013) so the diversity found in contemporary Antarctic benthic taxa is thought to have been generated via multiple isolation events during glacial maxima and minima (Allcock & Strugnell 2012). Nominal holothurian species recorded either side of the ACC were found to have distinct lineages suggesting no gene flow between these populations (and thus potentially great undescribed diversity), but no clear pattern was discernible as to the origins of each taxonomic group (O'Loughlin et al. 2013). Further research on the relationship of *Primnoisis tasmani* to other *Primnoisis* species which may be present in the waters around South America and South Africa would be required to further test this theory on the origin of the genus.

Accurate and consistent species delineation is fundamental to these biogeographic conclusions and resulting management decisions. Currently many deep-sea octocoral species are poorly defined and inaccurately named, and accordingly many recorded distributions are wrong. Taxonomic revisions such as this thesis form the essential foundations upon which future ecological and evolutionary studies are based.

5.4 Future directions

This thesis has highlighted and resolved some significant inaccuracies within our current understanding of octocoral taxonomic boundaries and definitions. In doing so it also identifies possible directions which will enhance and expedite future research on octocoral systematics:

- An urgent and well-recognised requirement is appropriately variable and reliably sequenced genetic markers within octocorals, particularly in the nuclear genome. Currently used gene regions are not variable enough to consistently delineate species nor to facilitate population level research. Ongoing research on microsatellites and SNPs utilising next-generation sequencing techniques (Reitzel et al. 2013) will quickly expand our knowledge of the genome and these regions should be explored for phylogenetic information.
- Retrospective investigation of morphological characteristics which correspond to molecular clades would build a more robust understanding of octocoral systematics and may facilitate the untangling of the many polyphyletic families and genera remaining.
- The exploration of additional or underutilised morphological characteristics such as the form and positioning of nematocysts (e.g. Yoffe, Lotan, & Benayahu 2012), node or internode construction (e.g. Alderslade 1998), reproductive modes (e.g. Kahng et al. 2011), colony colour, and techniques such as morphometrics (e.g. Carlo, Barbeitos, & Lasker 2011; Pante & Watling 2012) may provide insights into faunal relationships.
- True circumpolar distributions of *Primnoisis* species can only be confirmed with additional specimens, especially from around the Antarctic Peninsula. Increased sampling effort in Antarctica is an expensive and practically difficult task (as is any research on deep-sea environments) but collaboration between institutions and scientists in order to share

samples and sequences can greatly increase access to these valuable resources and ultimately will produce more robust science.

5.5 Concluding remarks

This thesis undertook to taxonomically review two deep-sea octocoral genera, chosen due to the evident confusion and uncertainty inherent within each genus and the difficultly associated with confidently assigning species (or even genus) to relevant specimens. Combining morphological and molecular approaches significantly strengthened the conclusions and can provide some optimism for future efforts to clarify taxonomic placements and relationships within the octocoral fauna. However, the (at present) insurmountable limitation on combining morphological and molecular approaches is that species definitions are based on old and often small fragments of type specimens which effectively cannot be sequenced. The type specimen is the permanent and only template for that species and traditional species names cannot be correctly assigned without morphological assessments and comparisons with the type specimen. Moreover, in this study, sequences could only be obtained for a small proportion of the available specimens and thus morphological and geographical characteristics were often the only available option for species designation. This obviously may change in the future but until then, morphological assessment and classical taxonomic revision, with the essential but difficult subjective decisions on variation, must continue.

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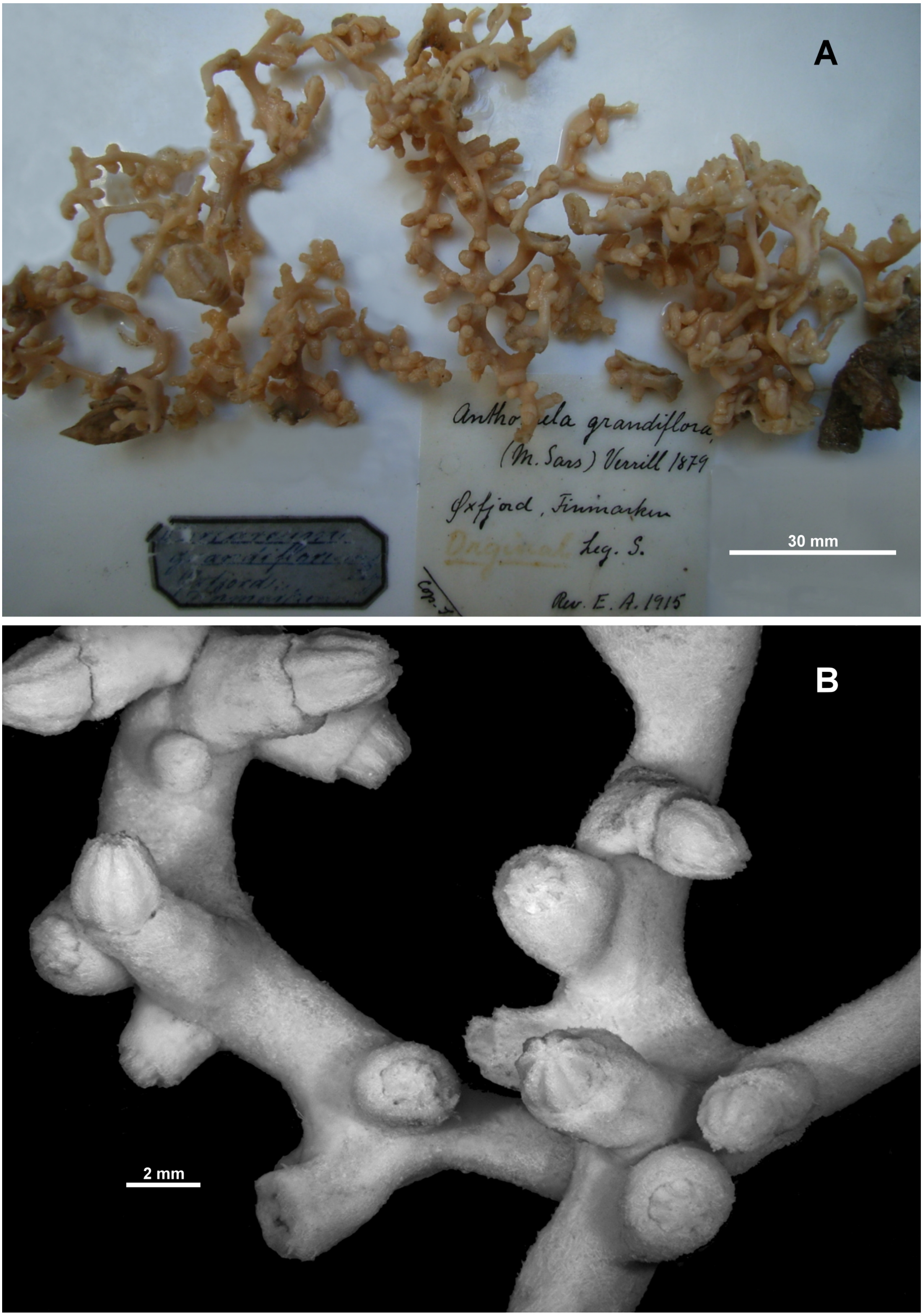

Figure 2.1. *Anthothela grandiflora* (Sars, 1856), holotype: A. Holotype fragments; B. Polyps and branches.

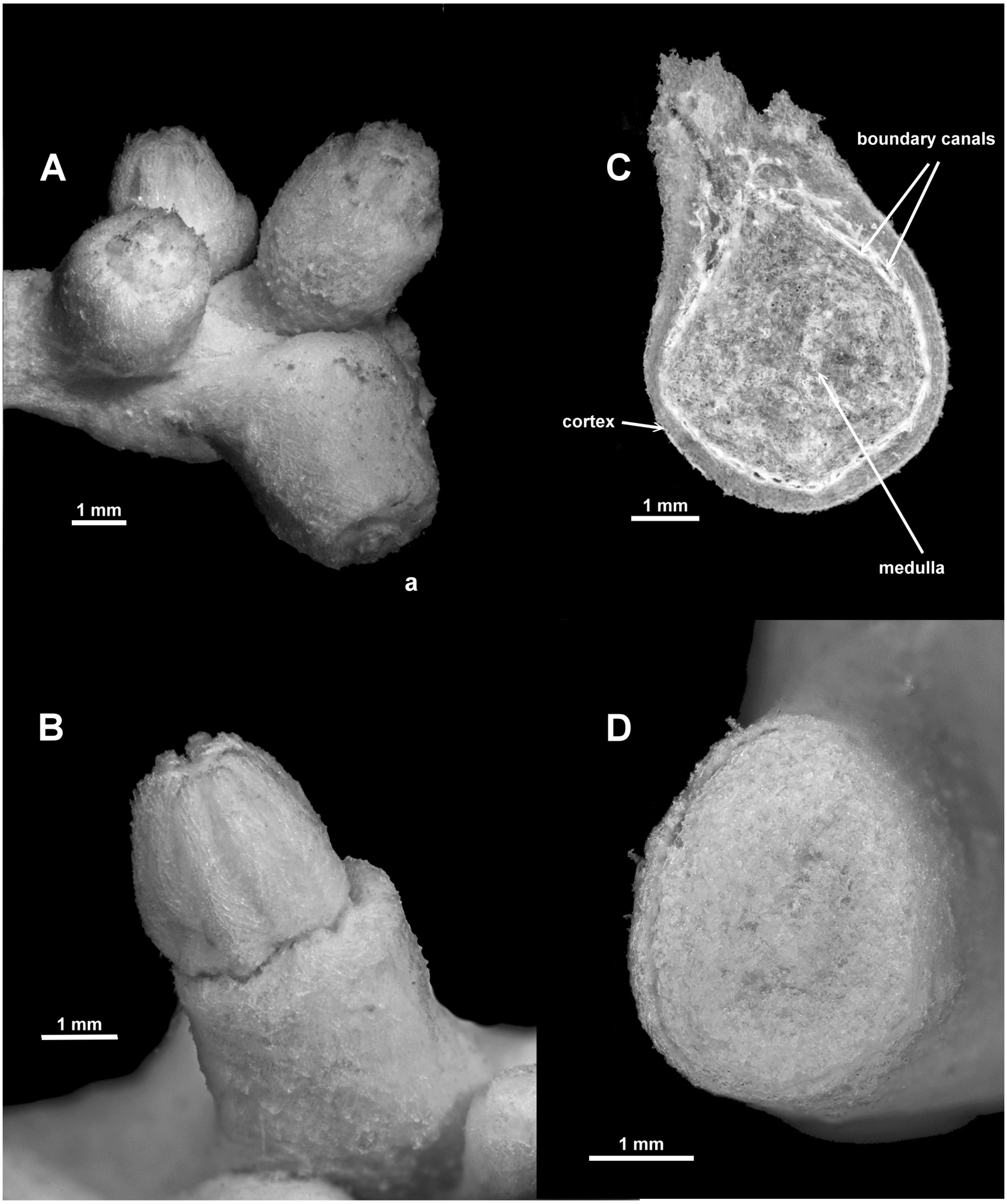

Figure 2.2. *Anthothela grandiflora* (Sars, 1856), holotype: A. Terminal polyp bunch (a. fully retracted polyp); B. Partly retracted polyp; C. Cross-section of decalcified medulla; D. Cross-section of medulla.

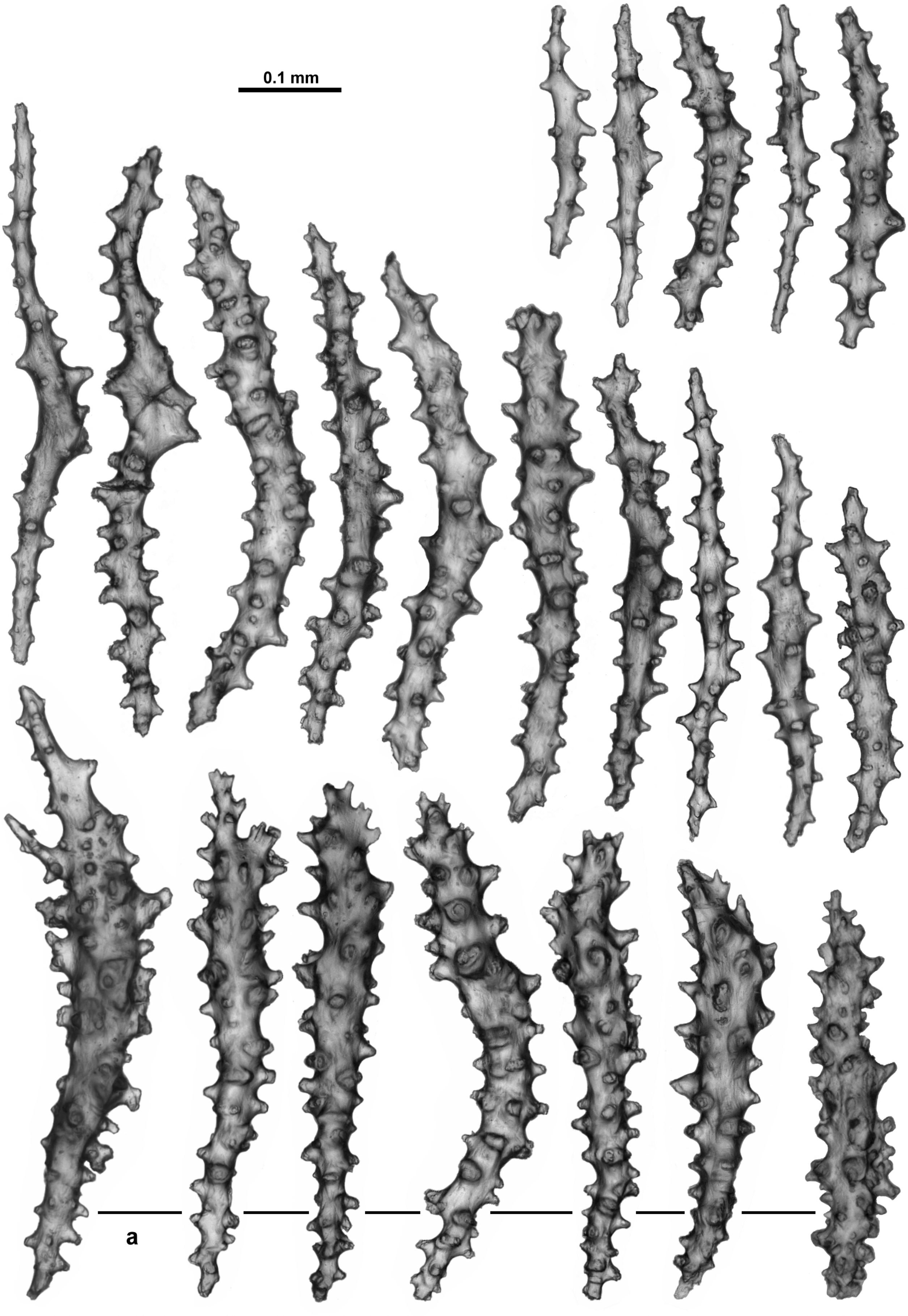

Figure 2.3. *Anthothela grandiflora* (Sars, 1856), holotype, sclerites: Point and collaret (a. sclerites with slightly more developed tips).

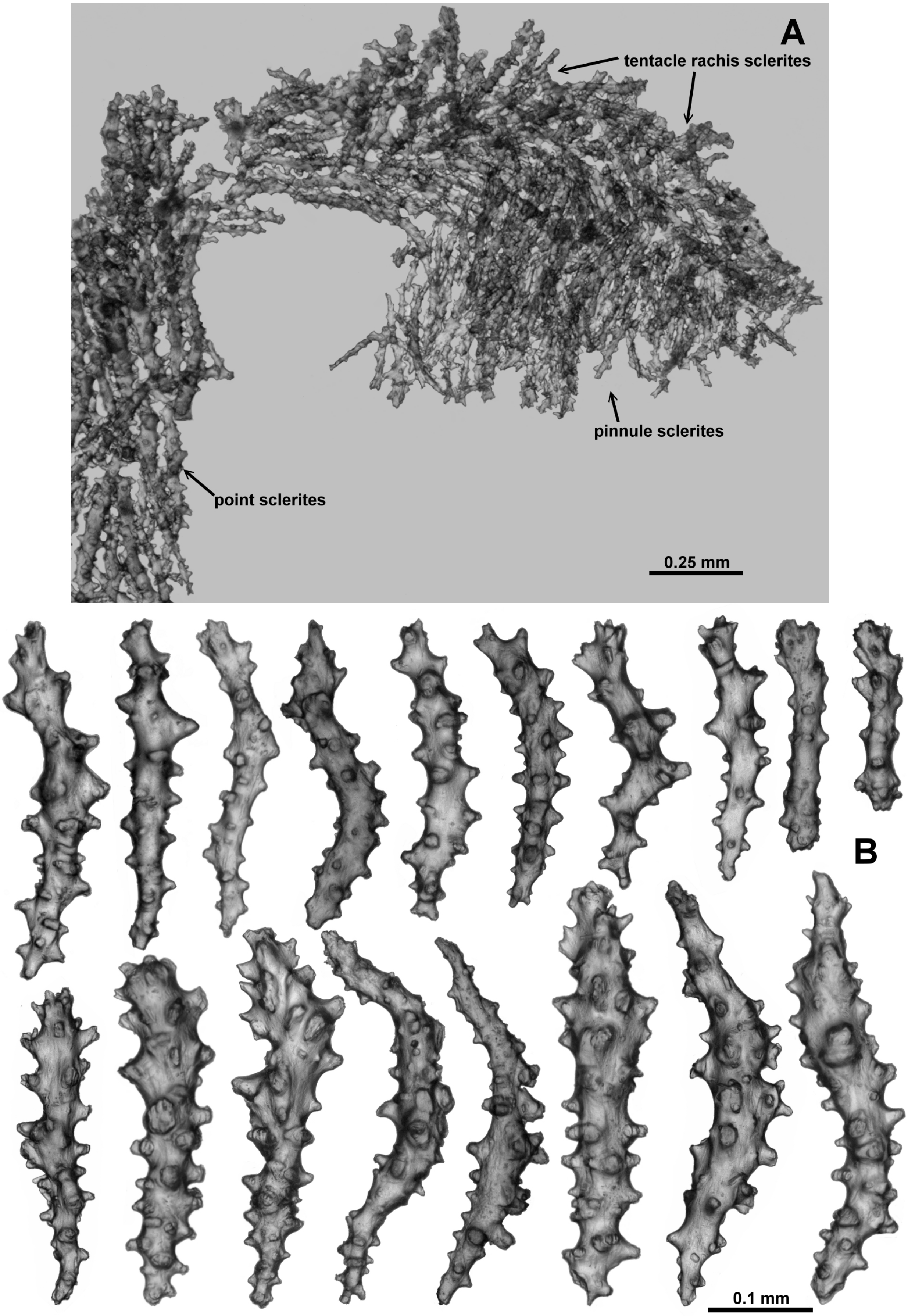

Figure 2.4. *Anthothela grandiflora* (Sars, 1856)*,* holotype: A. Tentacle and points sclerites in situ; B. Tentacle rachis sclerites.

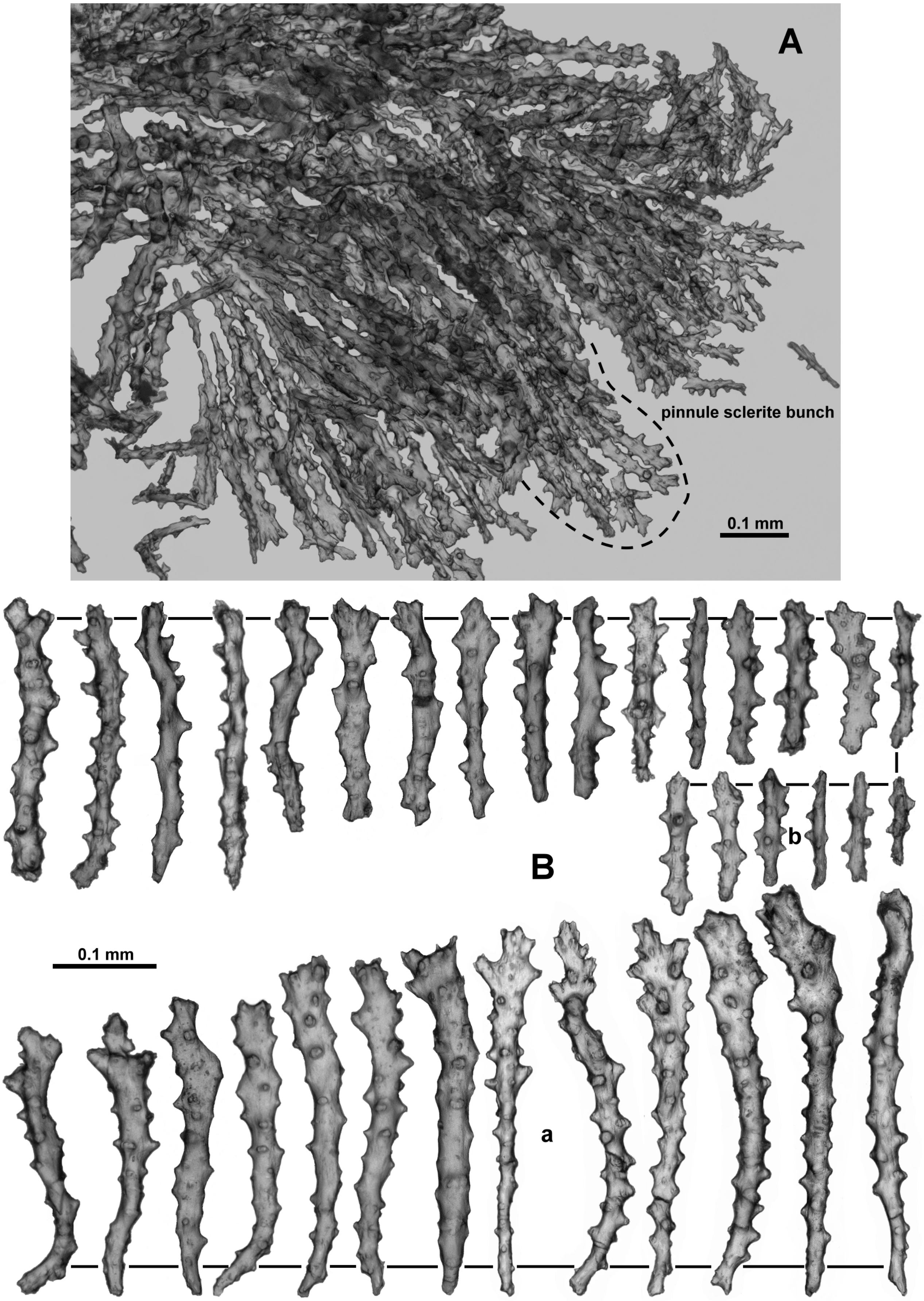

Figure 2.5. *Anthothela grandiflora* (Sars, 1856), holotype: A. Tip of cleared tentacle showing crowded sclerites in pinnules; B. Pinnule sclerites (a. spatulate clubs; b. rods, simple spindles and flanged spindles).

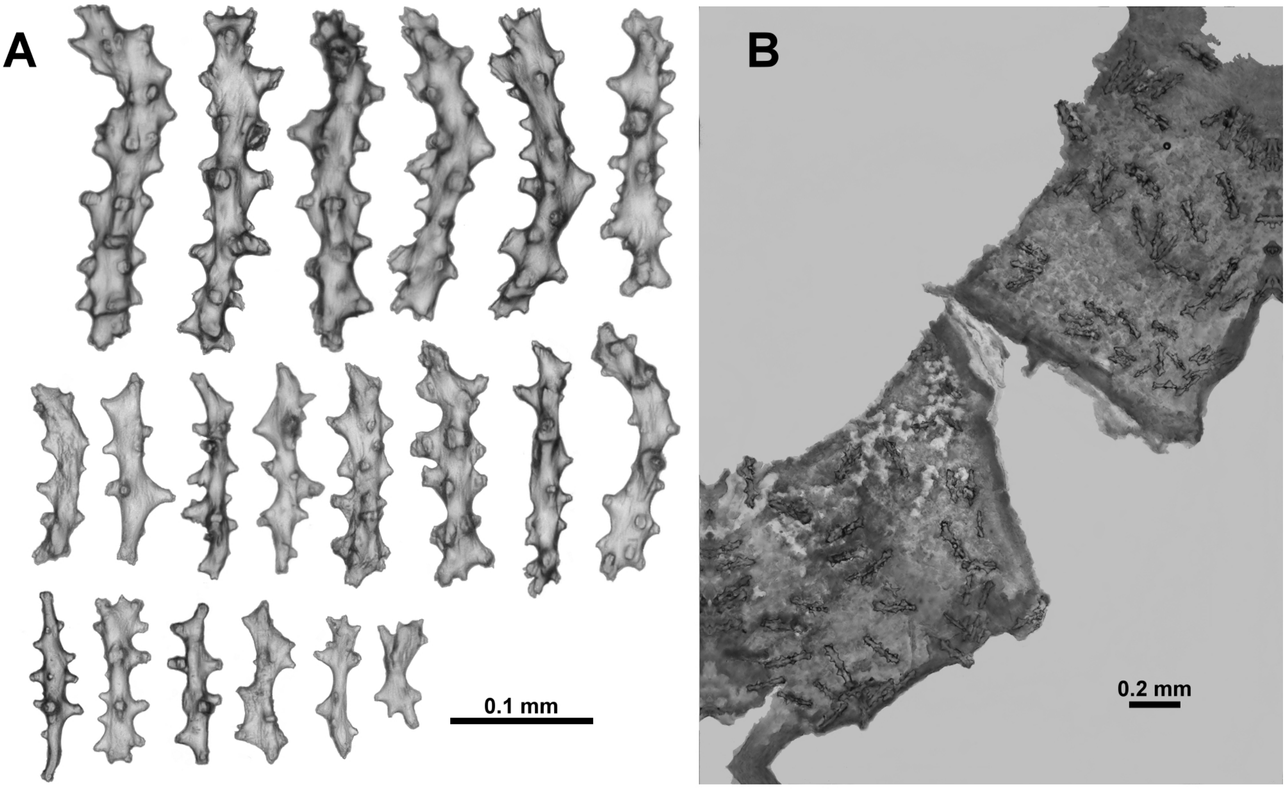

Figure 2.6. *Anthothela grandiflora* (Sars, 1856), holotype: A. Pharynx sclerites; B. In situ arrangement of pharynx sclerites.

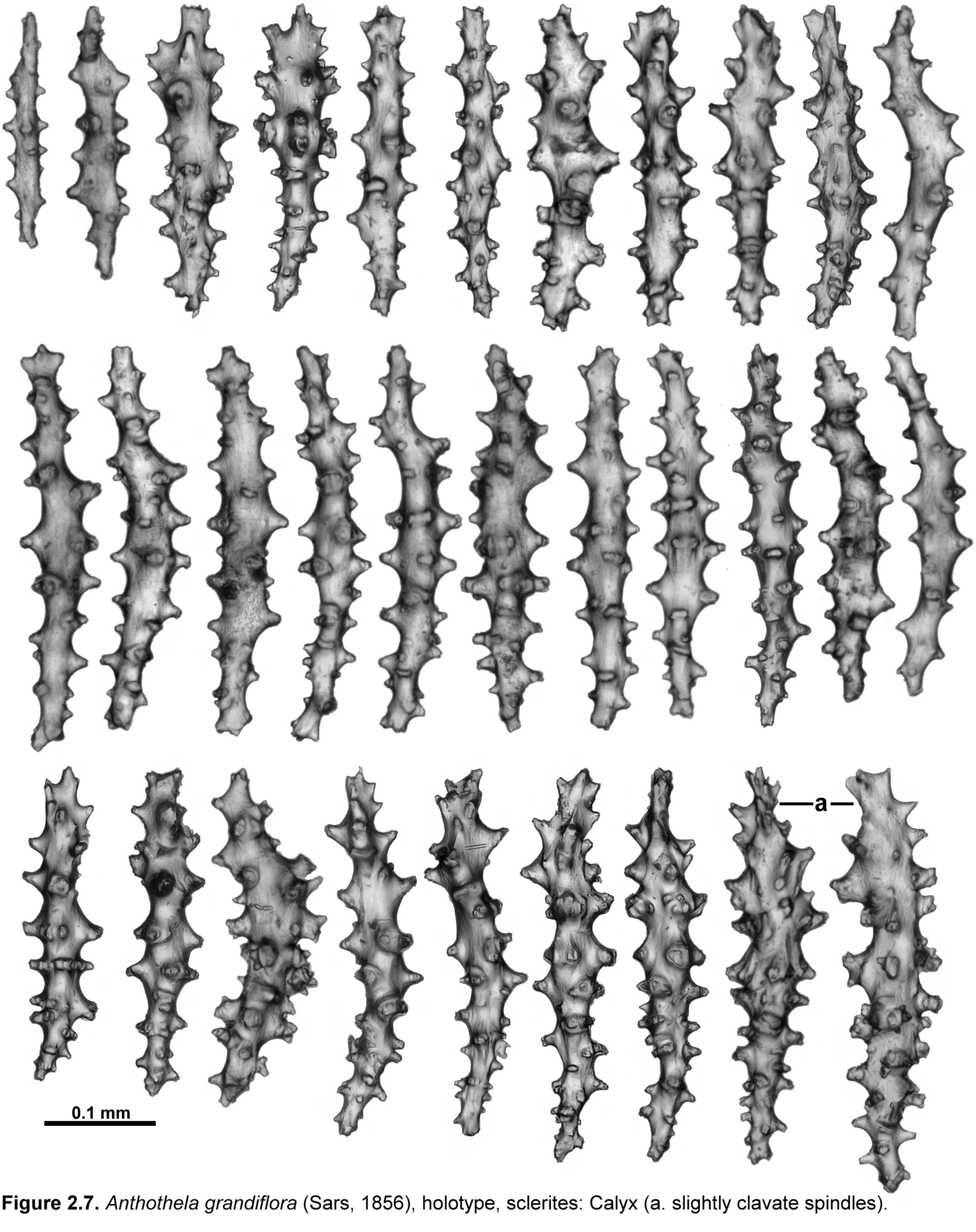

Figure 2.7. *Anthothela grandiflora* (Sars, 1856), holotype, sclerites: Calyx (a. slightly clavate spindles).

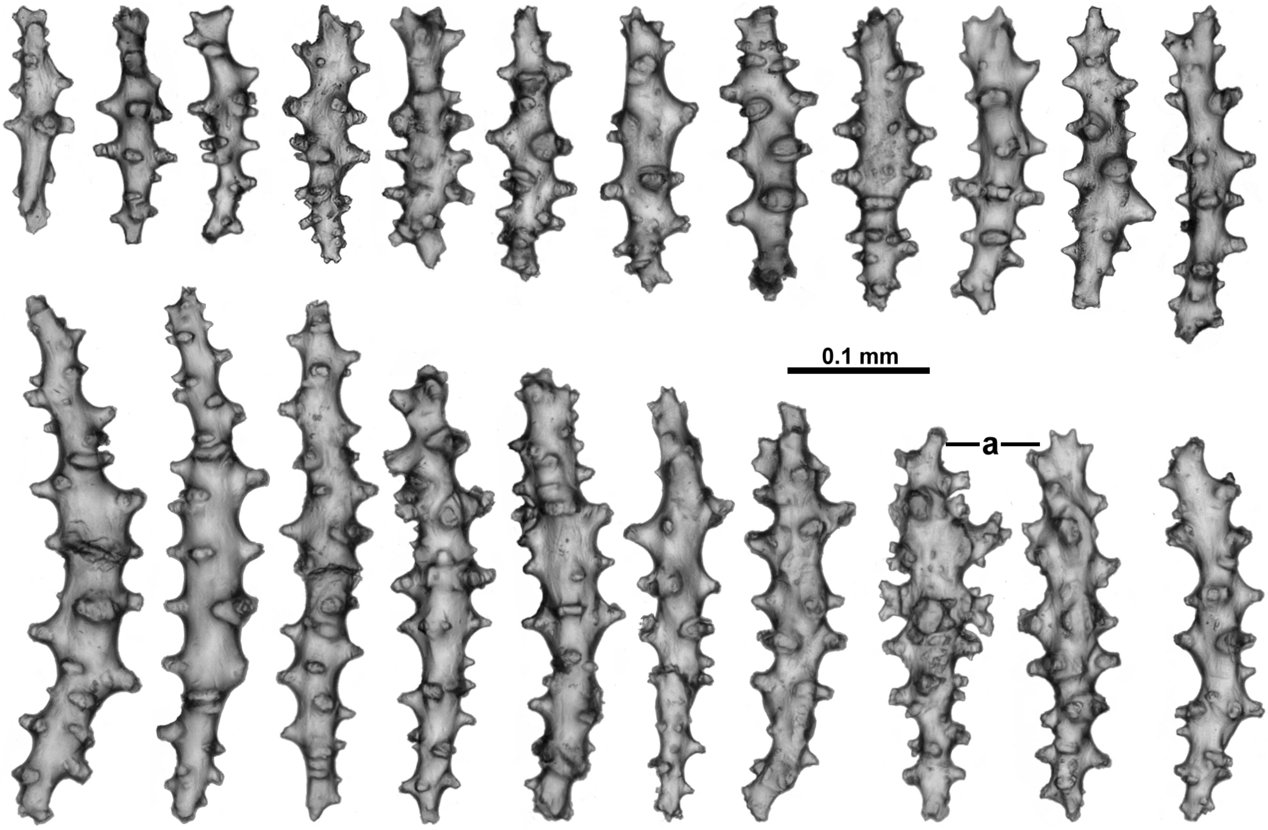

Figure 2.8. *Anthothela grandiflora* (Sars, 1856), holotype, sclerites: Cortex (a. slightly clavate sclerites).

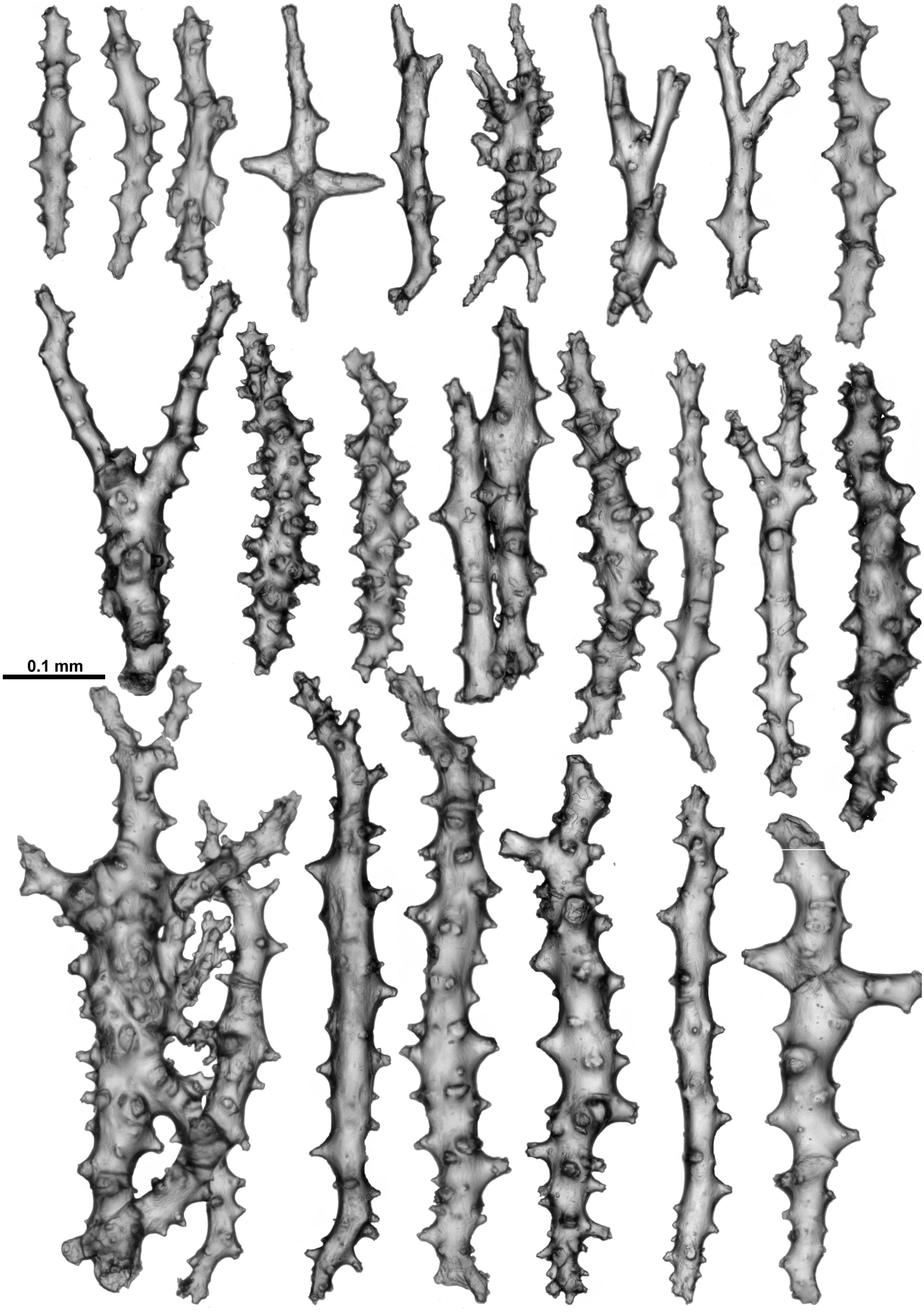

Figure 2.9. *Anthothela grandiflora* (Sars, 1856), holotype, sclerites: Medulla.

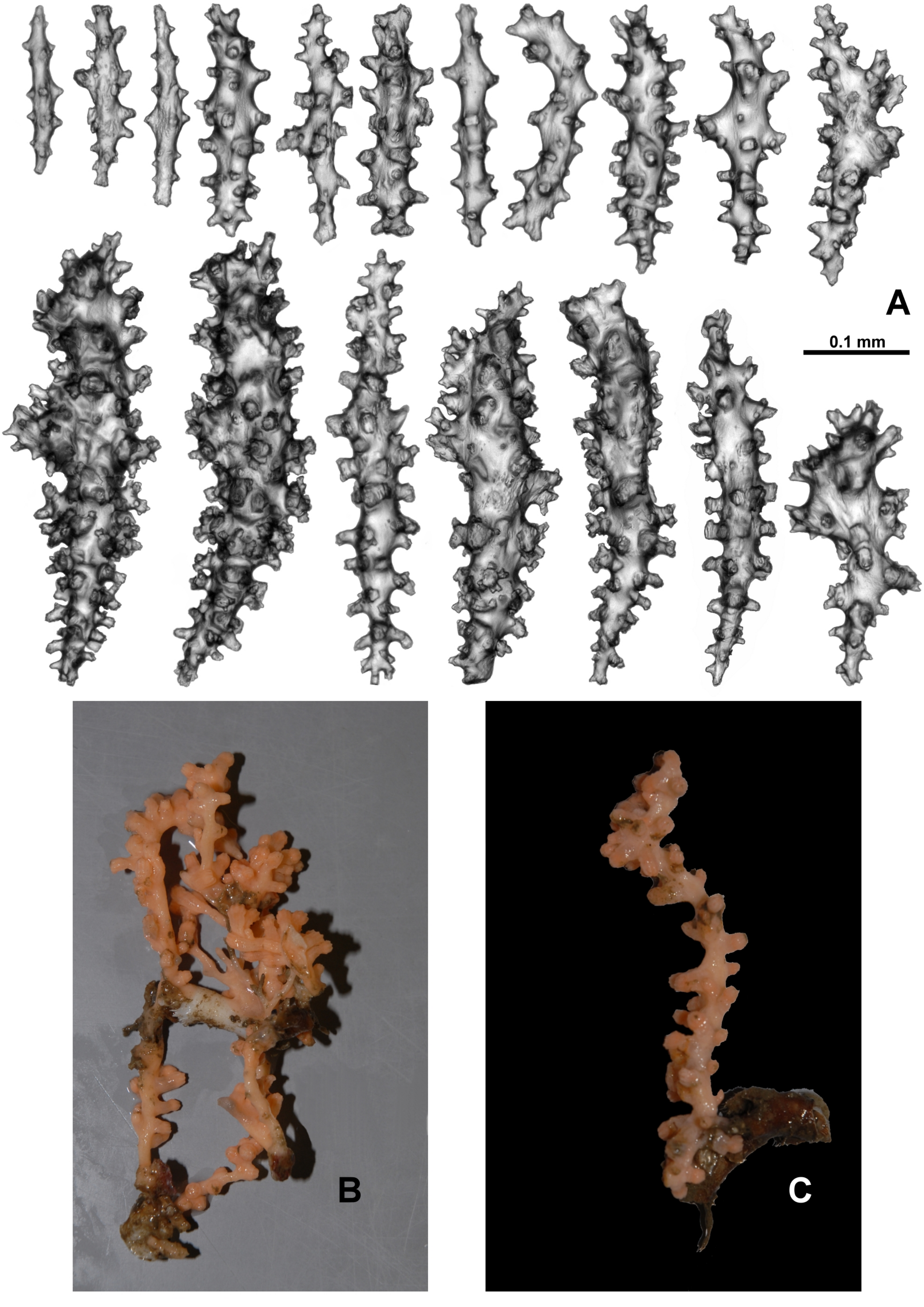

Figure 2.10. *Anthothela grandiflora* (Sars, 1856): A-B. NTNU 67149: (A). Calyx sclerites; (B). Recently collected colony. C. NTNU 67148, recently collected colony.

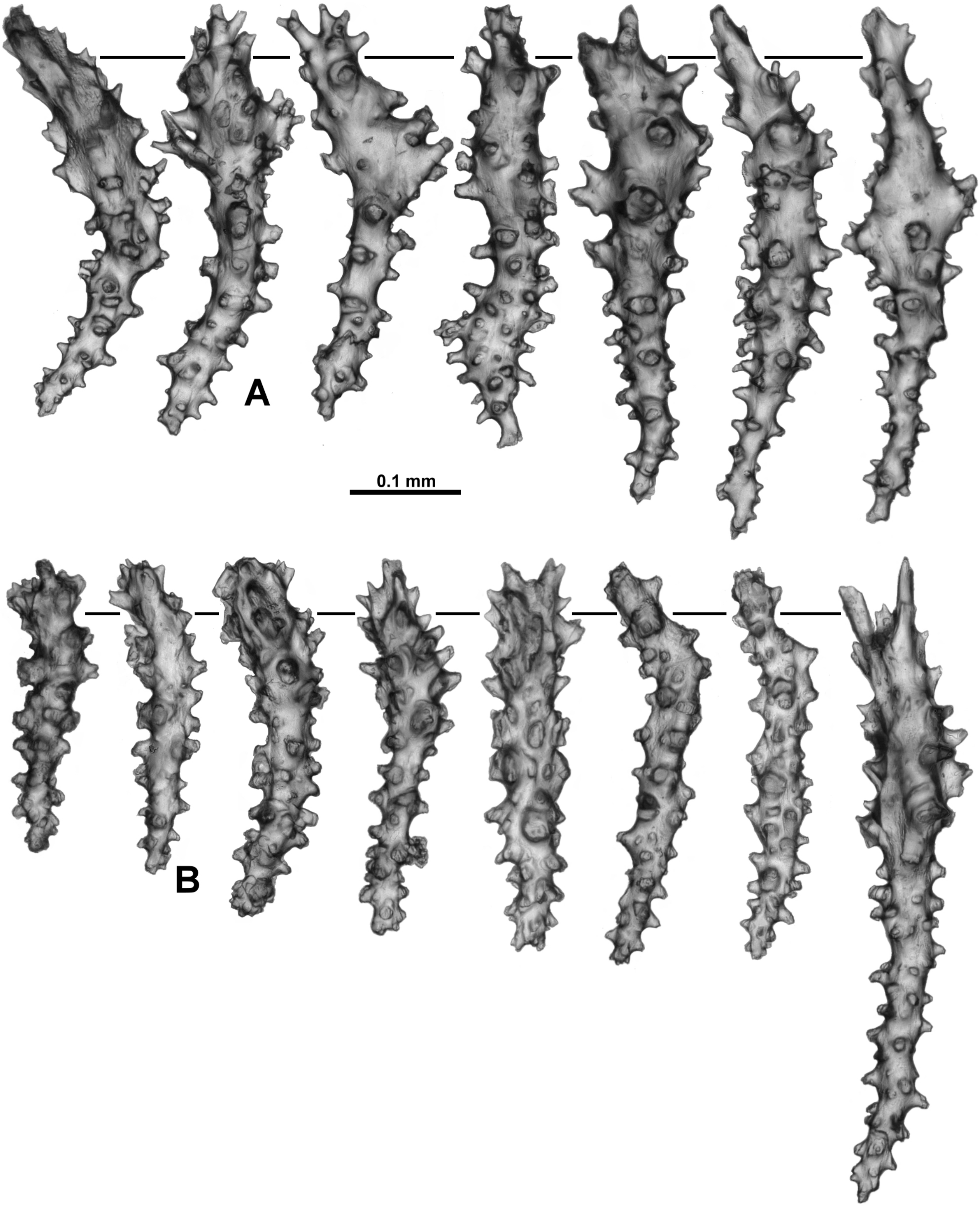

Figure 2.11. *Anthothela grandiflora* (Sars, 1856), tentacle sclerites: A. ZMUC-ANT-000470; B. NTNU 40338.

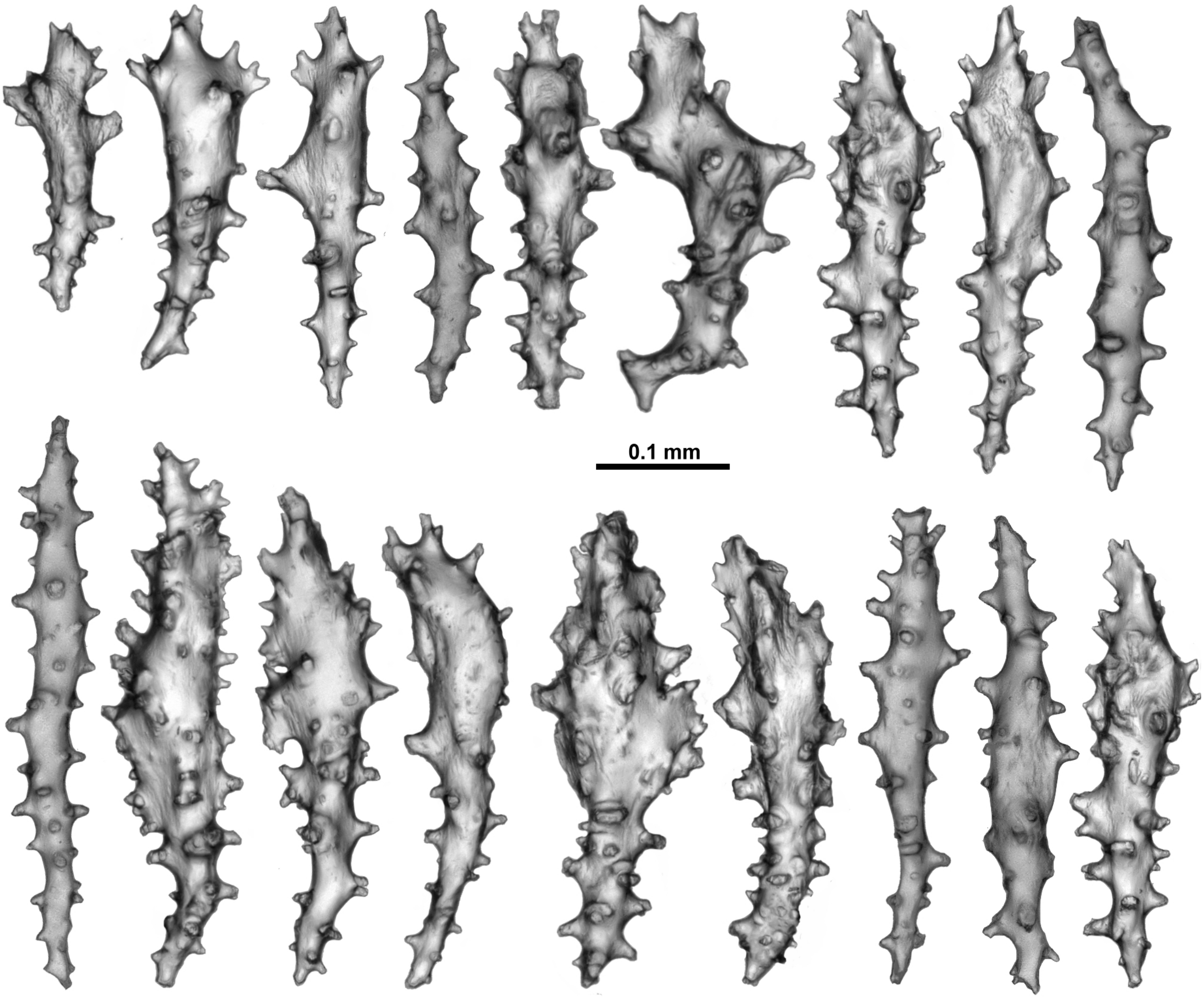

Figure 2.12. *Anthothela grandiflora* (Sars, 1856), NTNU 63139, sclerites: Cortex.

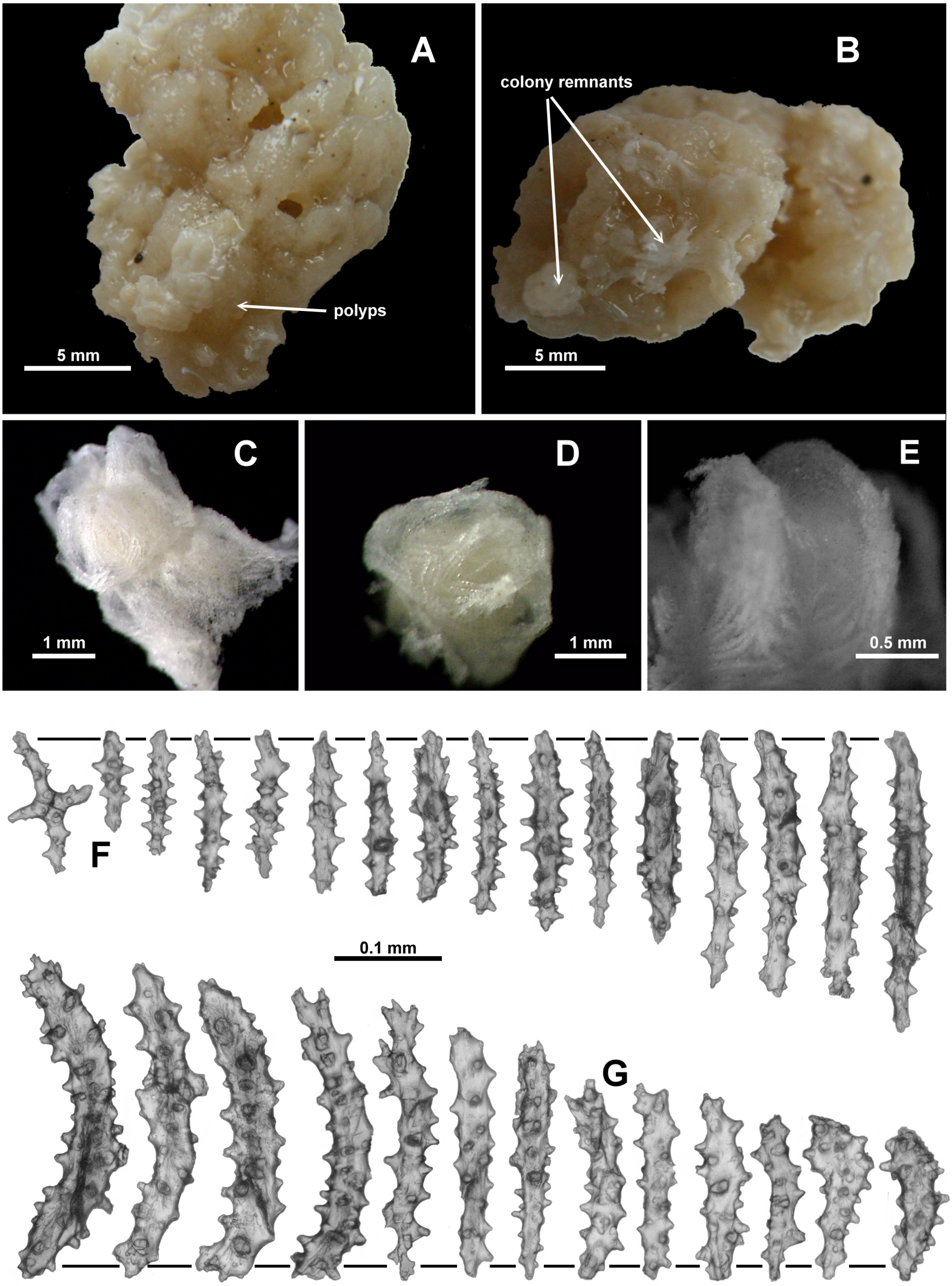

Figure 2.13. *Anthothela pacifica* (Kükenthal, 1913), lectotype: A-B. Sponge with *A. pacifica* colony remnants; C. Partly retracted polyp; D. Polyp head; E. Points arrangement; F. Point sclerites; G. Tentacle rachis sclerites.

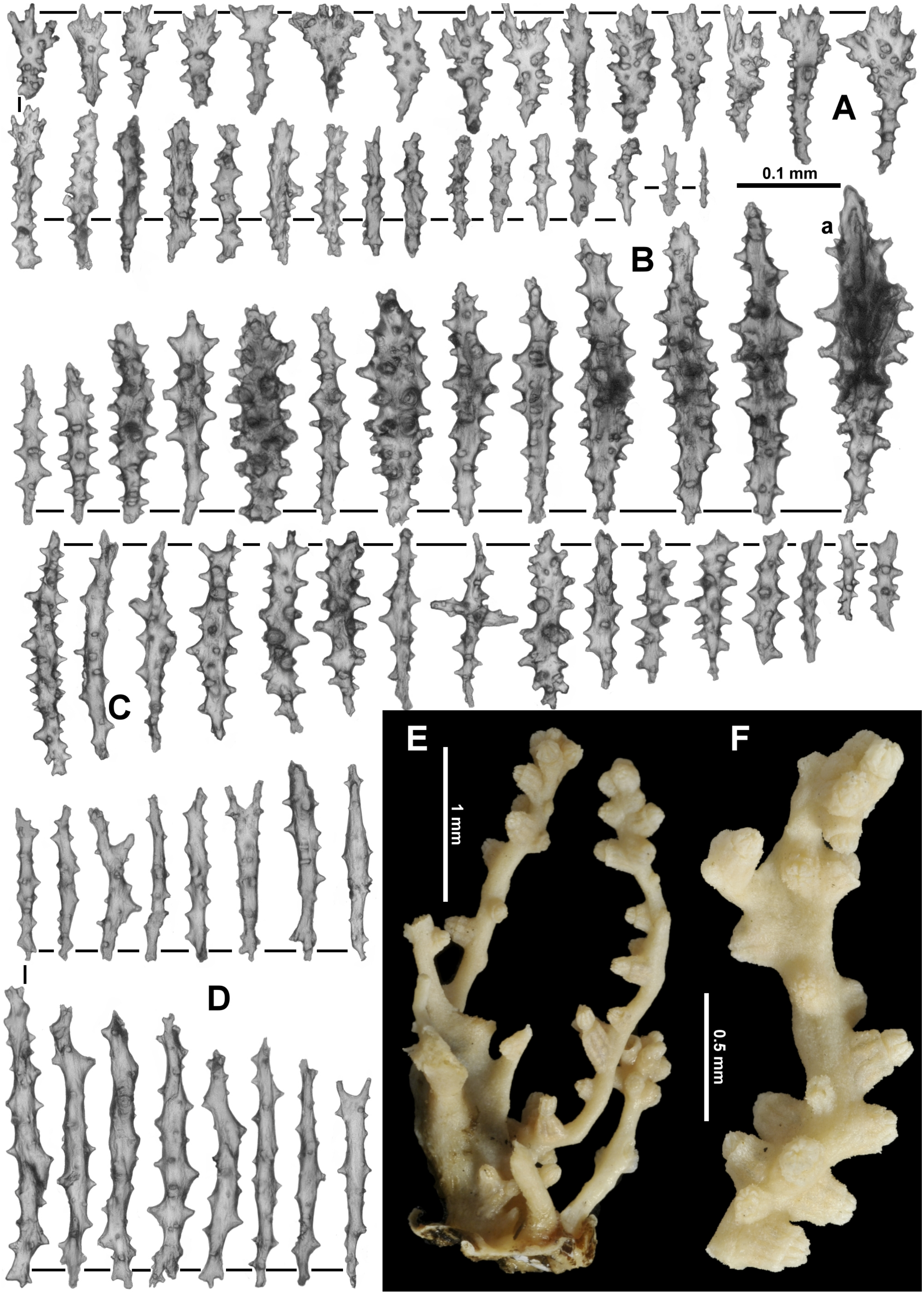

Figure 2.14. *Anthothela pacifica* (Kükenthal, 1913). A-D. Lectotype, sclerites: (A). Pinnule; (B). Calyx (a. straight club); (C-D). Cortex. E-F. USNM 57981: (E). Colony; (F). Branch fragment. (E-F. Courtesy of NMNH, Dr R. Ford).

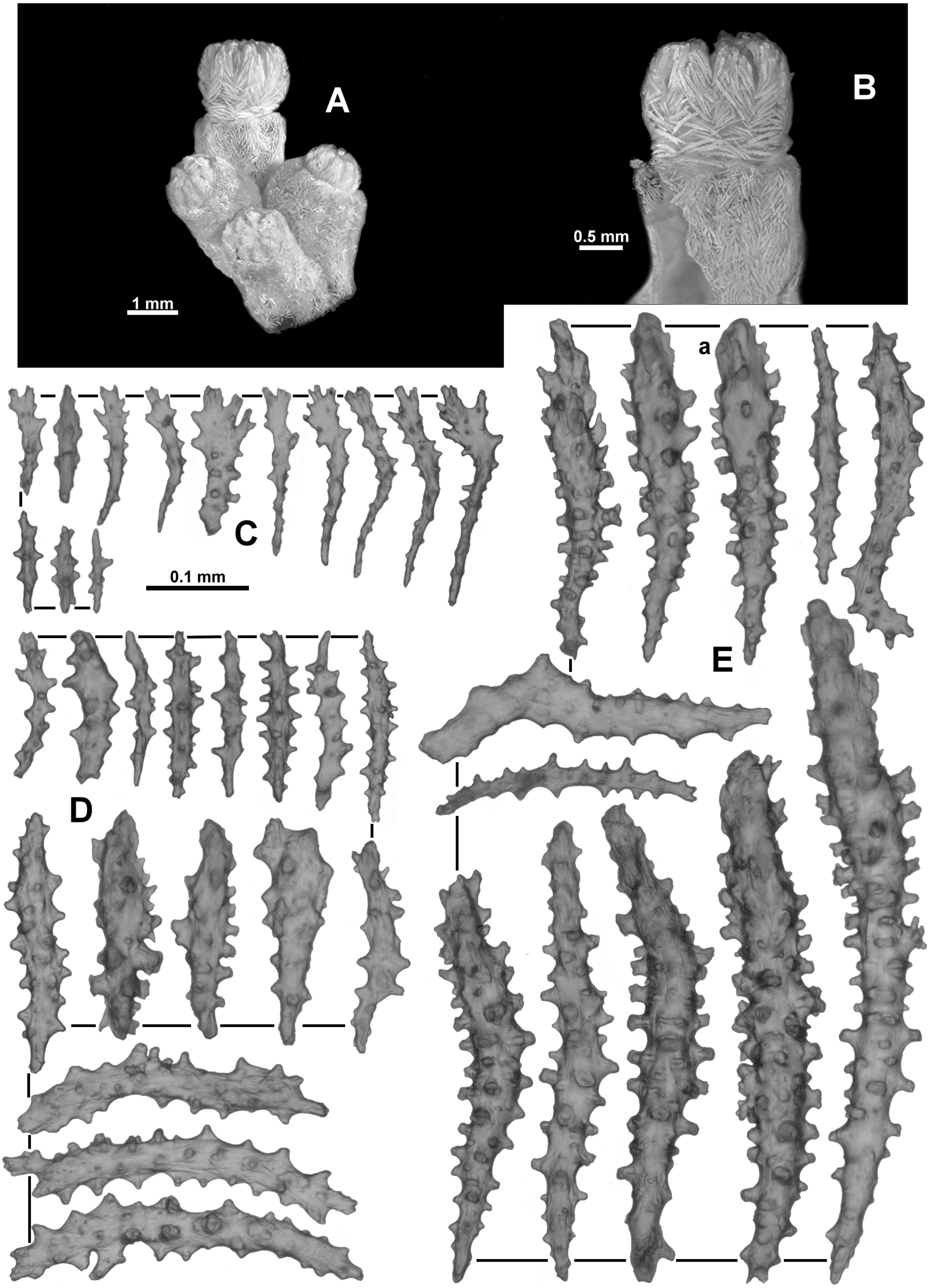

Figure 2.15. *Anthothela pacifica* (Kükenthal, 1913), USNM 57981: A. Terminal polyp bunch; B. Partly retracted polyp; C. Pinnule sclerites; D. Tentacle sclerites; E. Point sclerites (a. straight club).

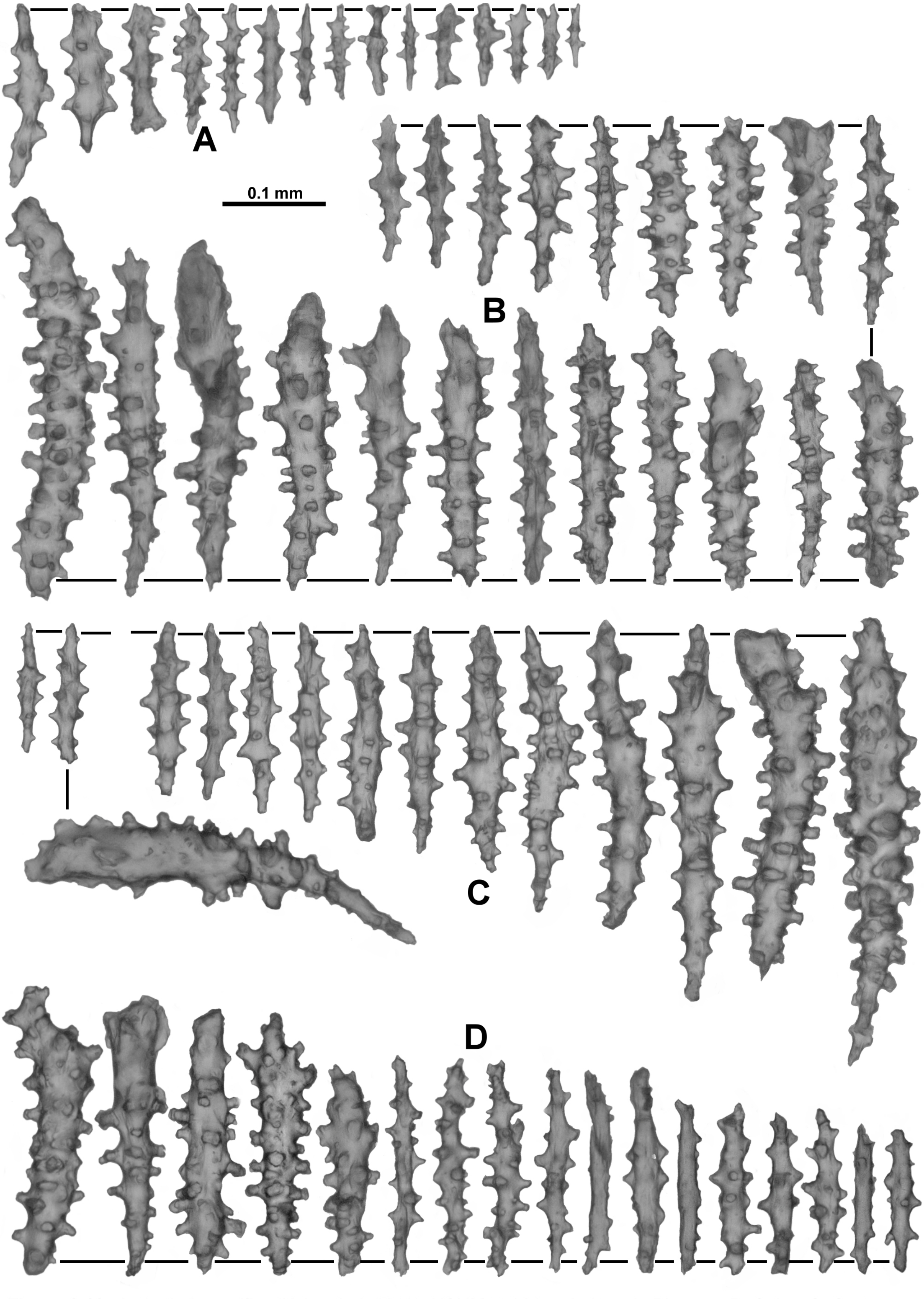

Figure 2.16. *Anthothela pacifica* (Kükenthal, 1913), USNM 57981, sclerites: A. Pharynx; B. Calyx; C. Cortex; D. Medulla.

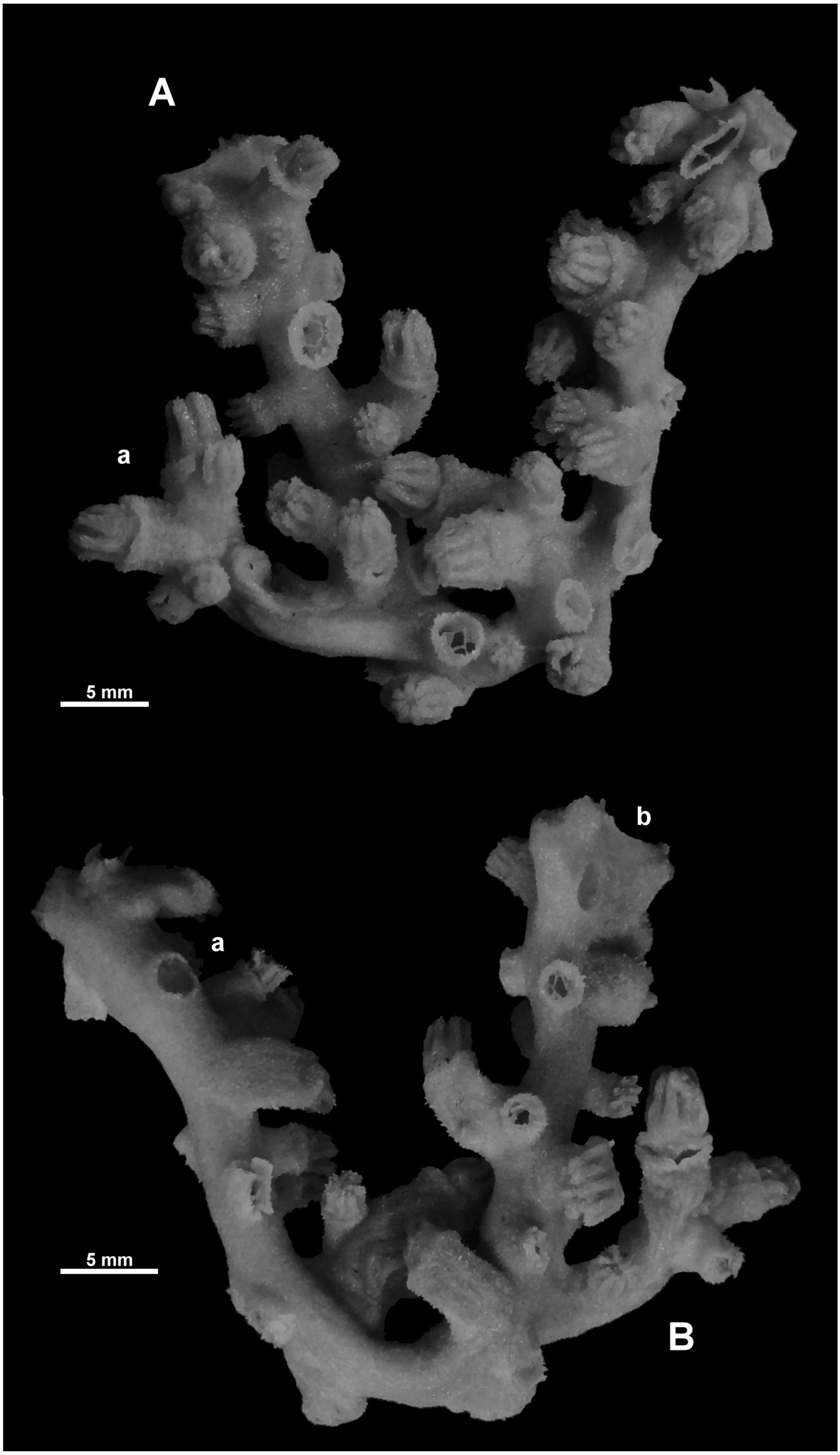

Figure 2.17. *Anthothela vickersi* (Benham, 1928), holotype: A-B. Different aspects of the colony (Aa. side branch Ba. possible dislodged polyp; Bb. evidence of broken side branch).

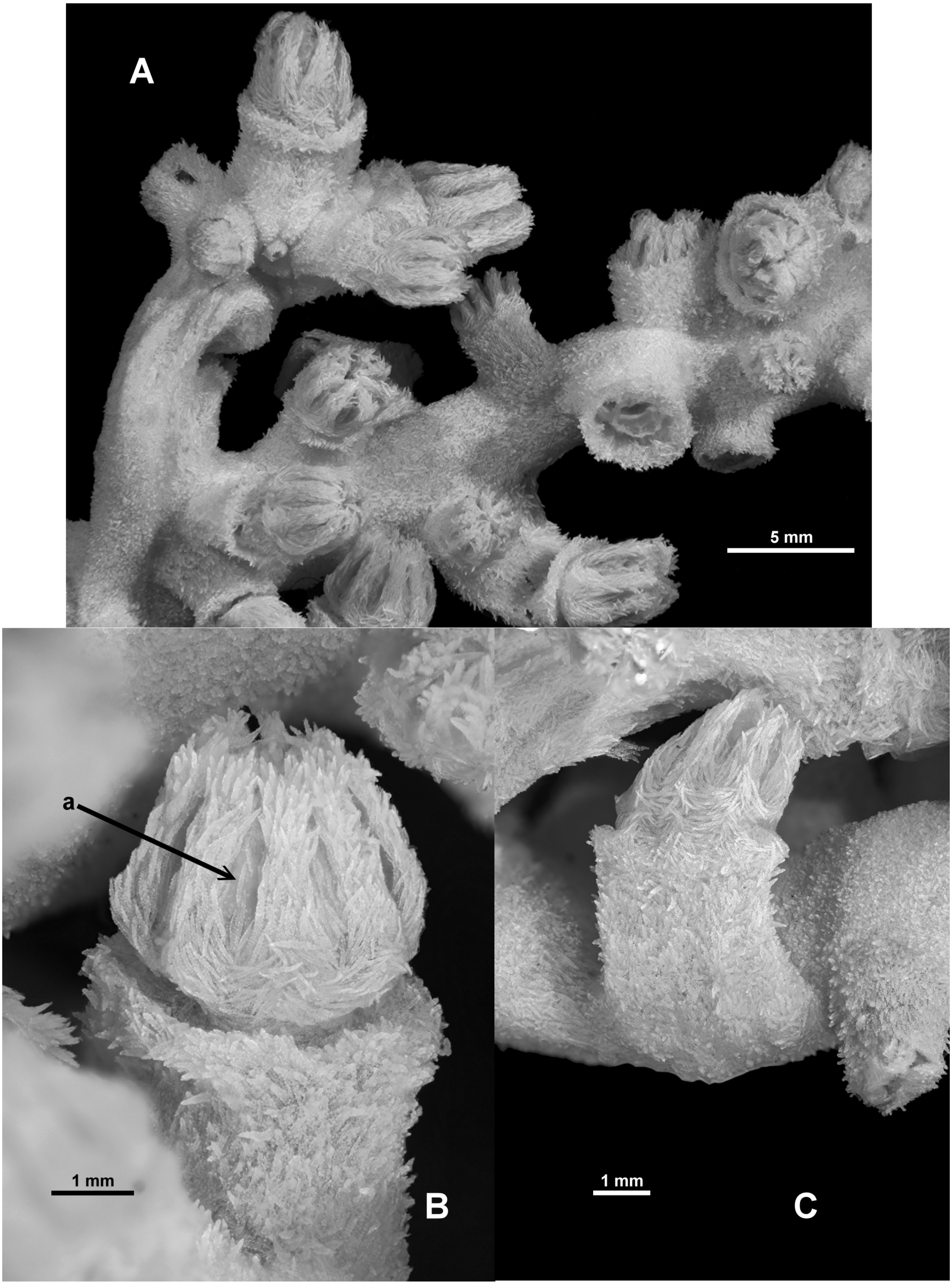

Figure 2.18. *Anthothela vickersi* (Benham, 1928), holotype: A. Branch with polyps; B. Partly retracted polyp (a. intermediate sclerites); C. Partly extended polyp.

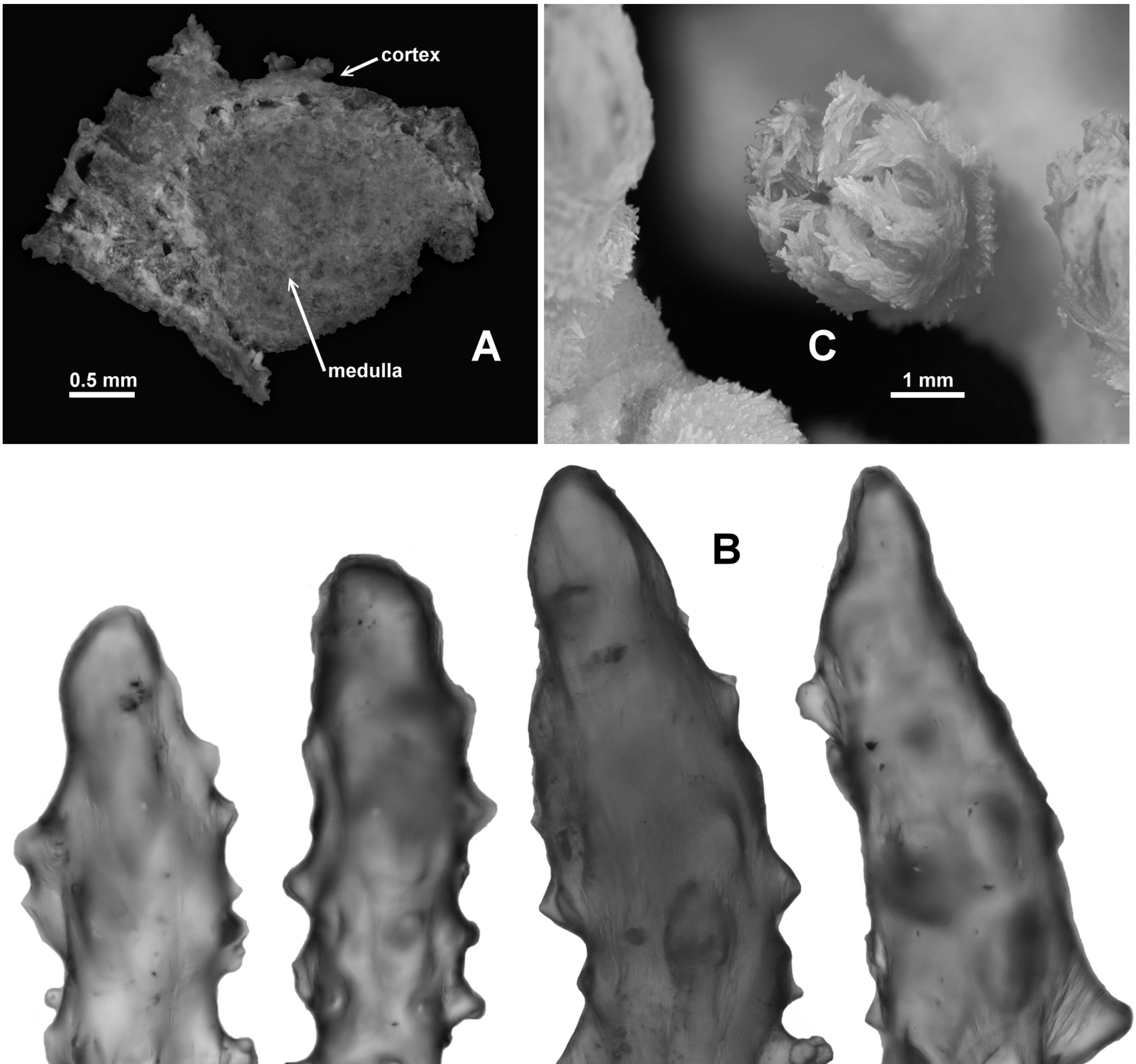

Figure 2.19. *Anthothela vickersi* (Benham, 1928)**,** holotype: A. Decalcified cross-section of medulla; B. Calyx sclerites with apparently damaged tips; C. Tentacles folded over polyp mouth.

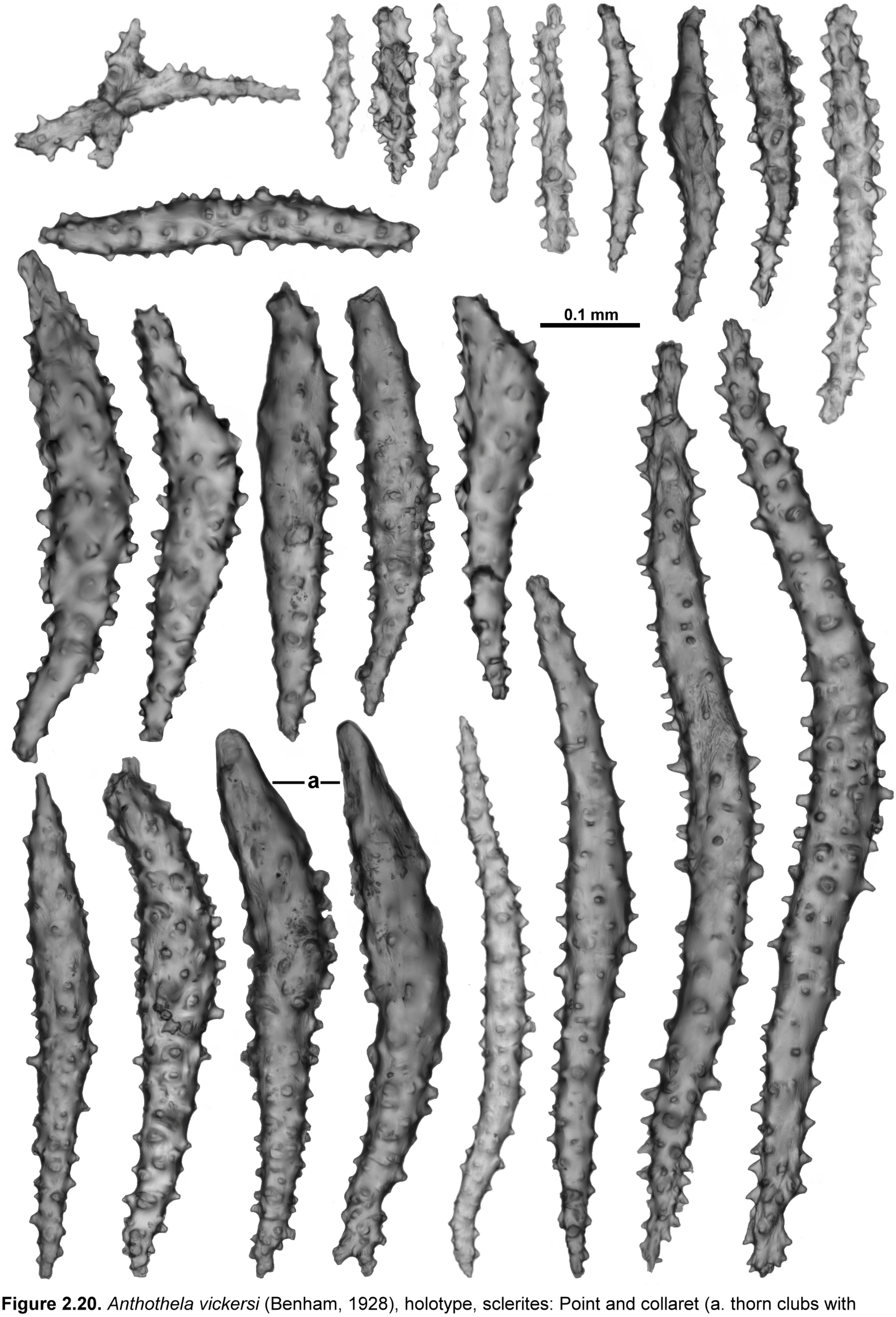

Figure 2.20. *Anthothela vickersi* (Benham, 1928), holotype, sclerites: Point and collaret (a. thorn clubs with smoothed tips).

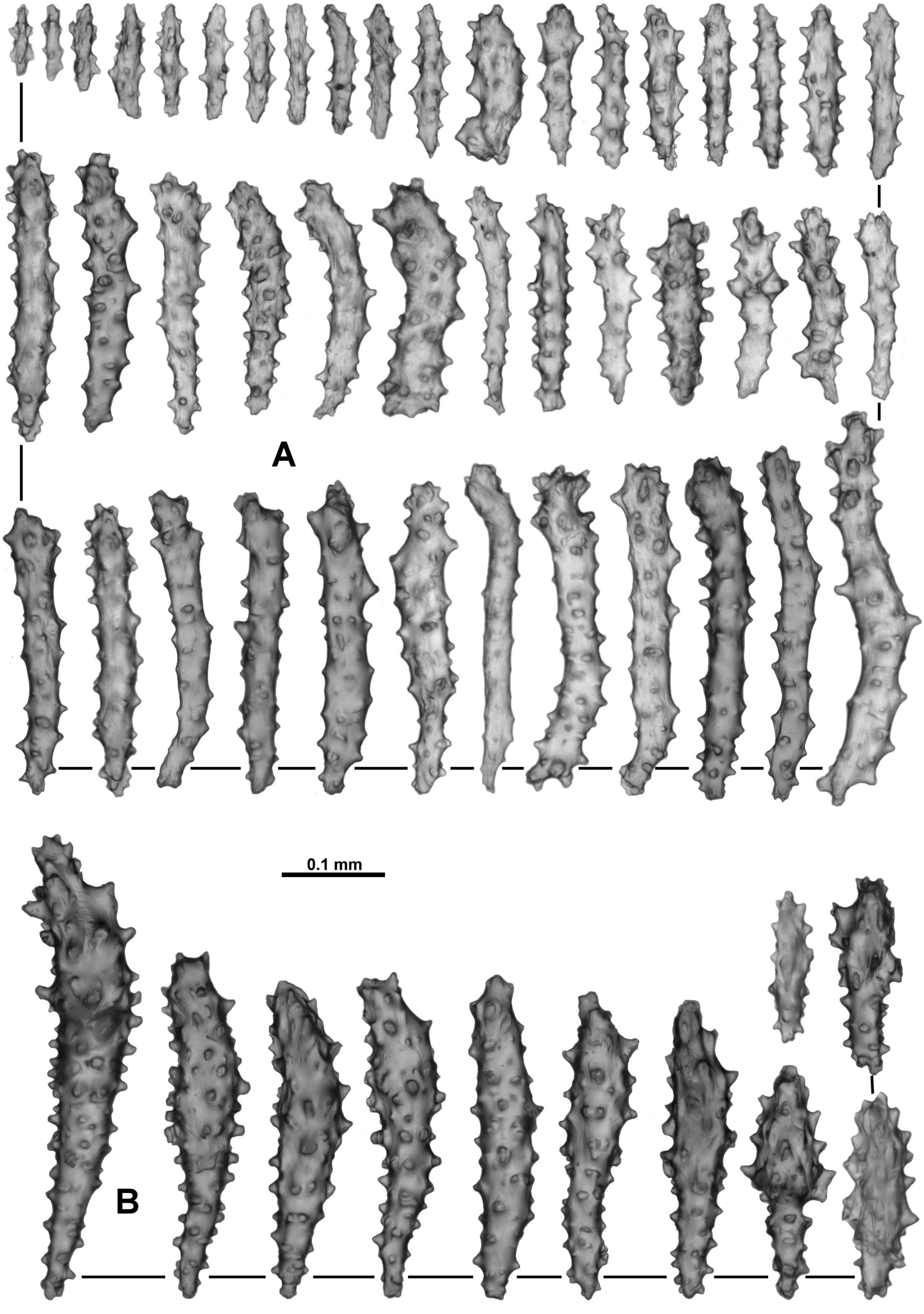

Figure 2.21. *Anthothela vickersi* (Benham, 1928), holotype, sclerites: A. Rods from tentacle rachis; B. Thorny clubs from tentacle rachis.

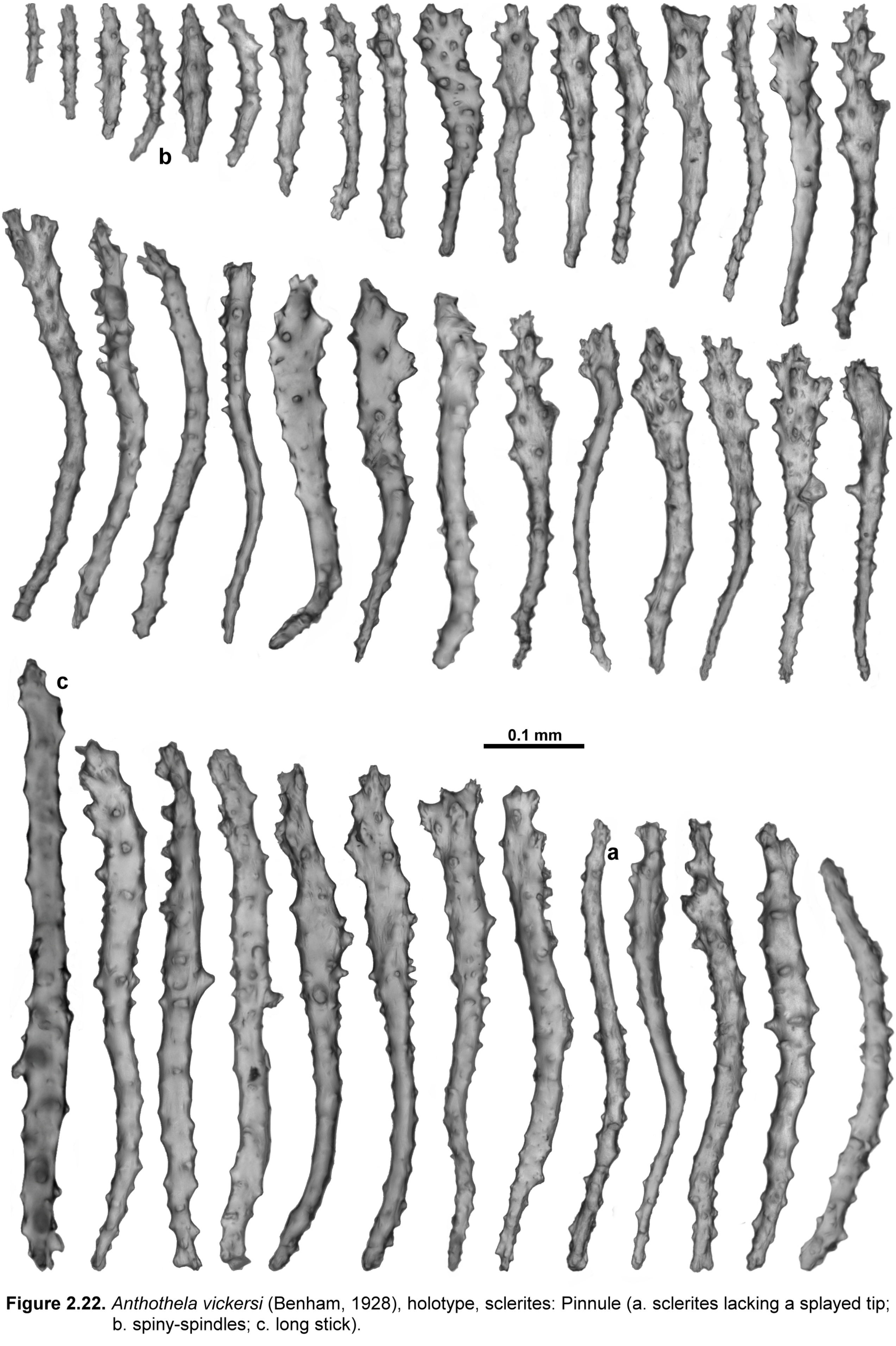

Figure 2.22. *Anthothela vickersi* (Benham, 1928), holotype, sclerites: Pinnule (a. sclerites lacking a splayed tip; b. spiny-spindles; c. long stick).

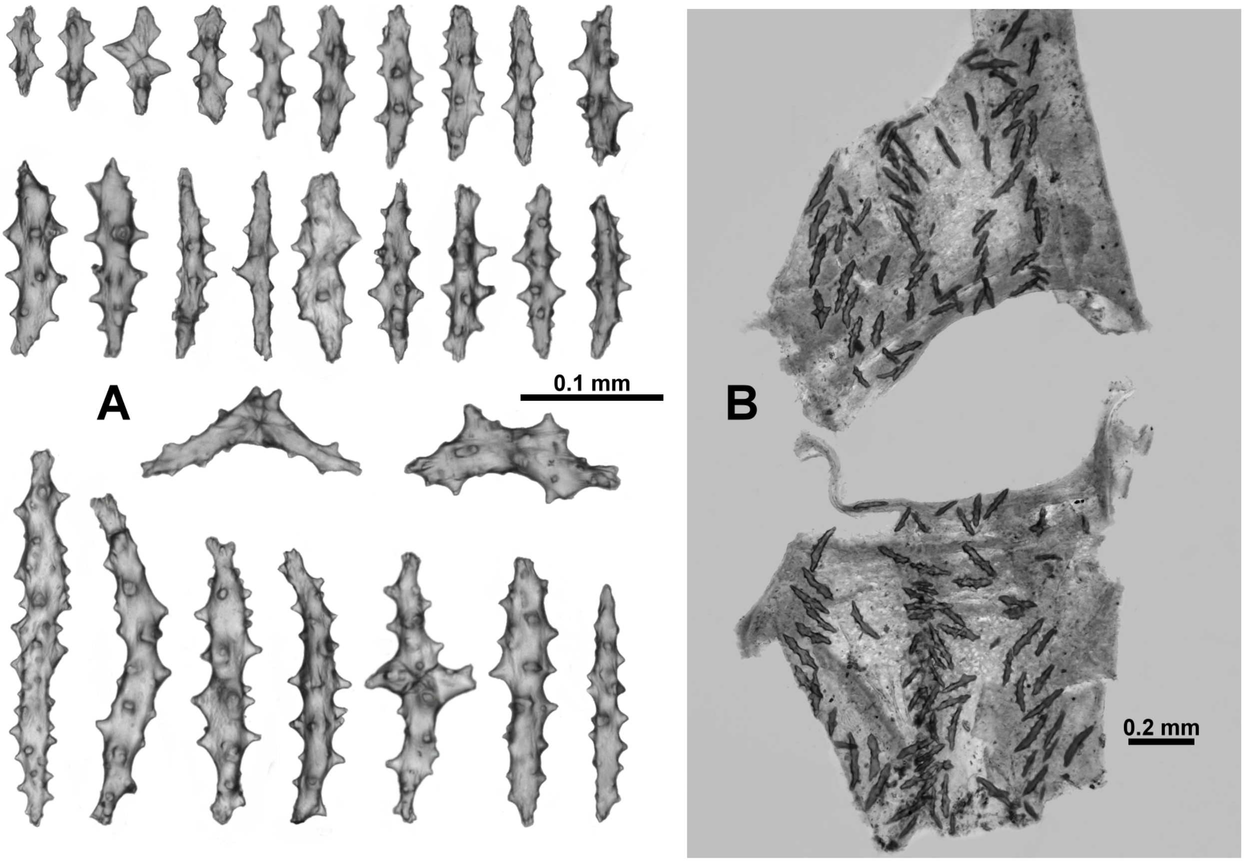

Figure 2.23. *Anthothela vickersi* (Benham, 1928), holotype: A. Pharynx sclerites; B. In situ arrangement of pharynx sclerites.

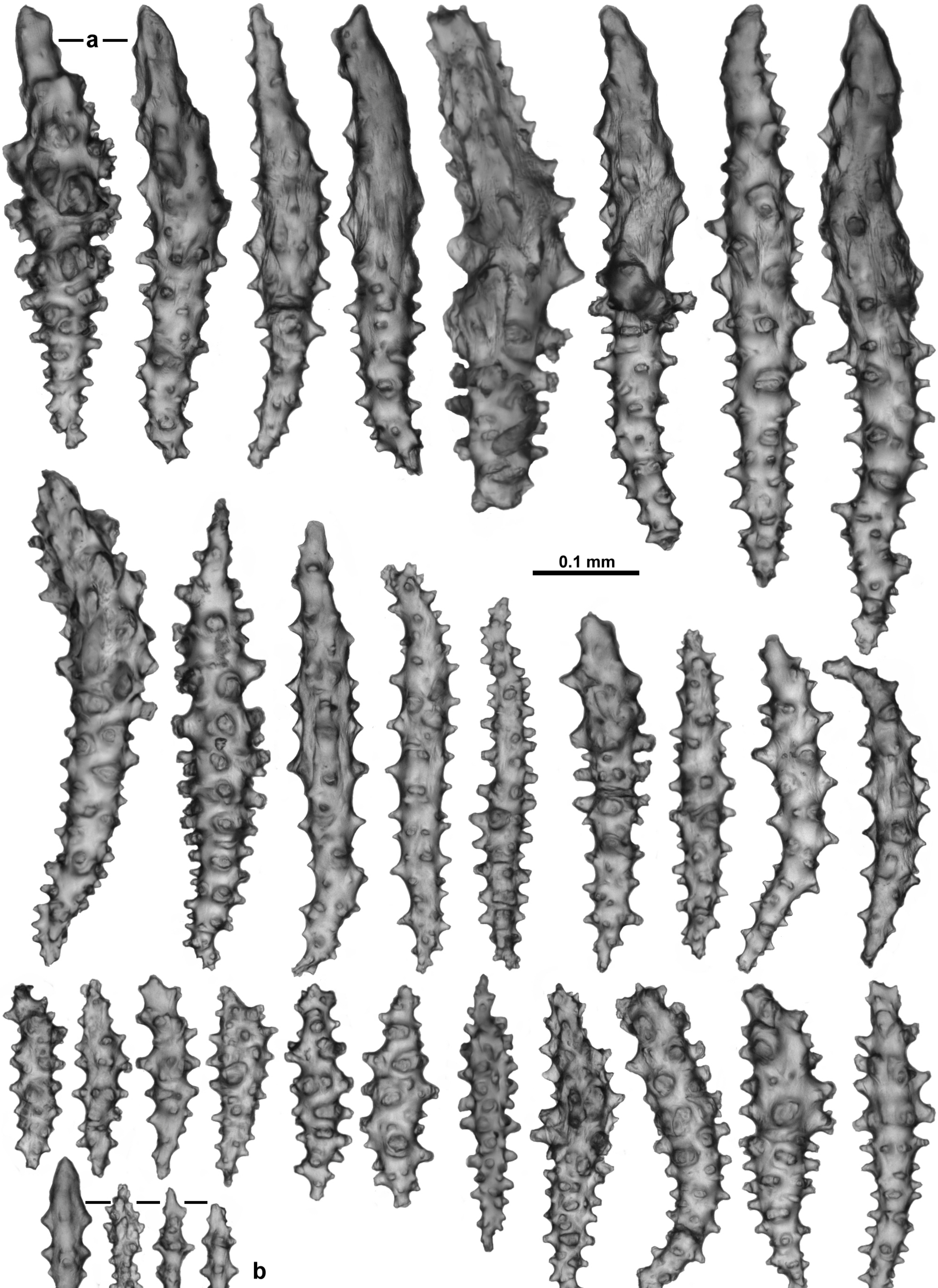

Figure 2.24. *Anthothela vickersi* (Benham, 1928), holotype, sclerites: Calyx (a. thorn clubs with slightly rounded tips; b. flanged spindles).

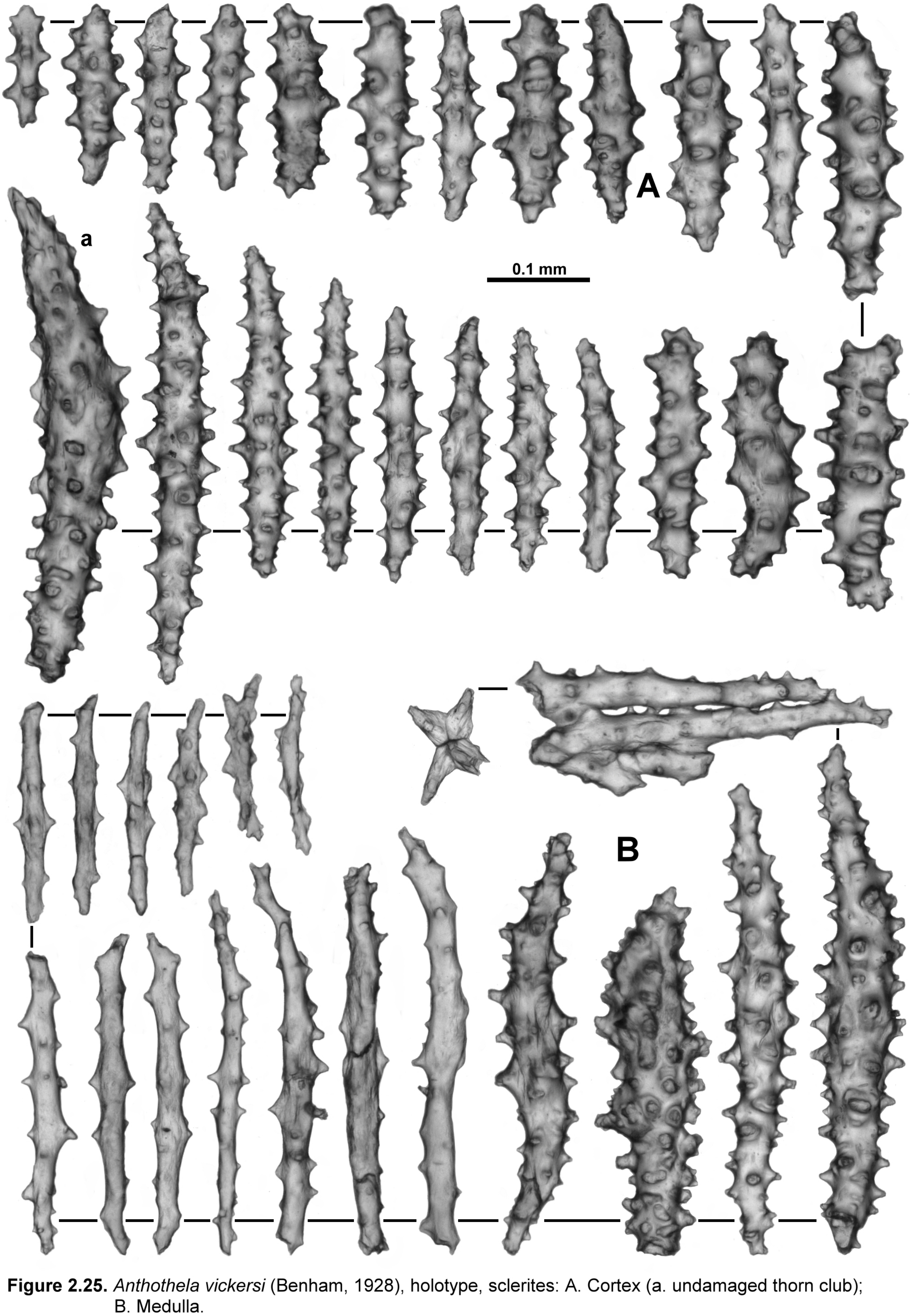

Figure 2.25. *Anthothela vickersi* (Benham, 1928), holotype, sclerites: A. Cortex (a. undamaged thorn club); B. Medulla.

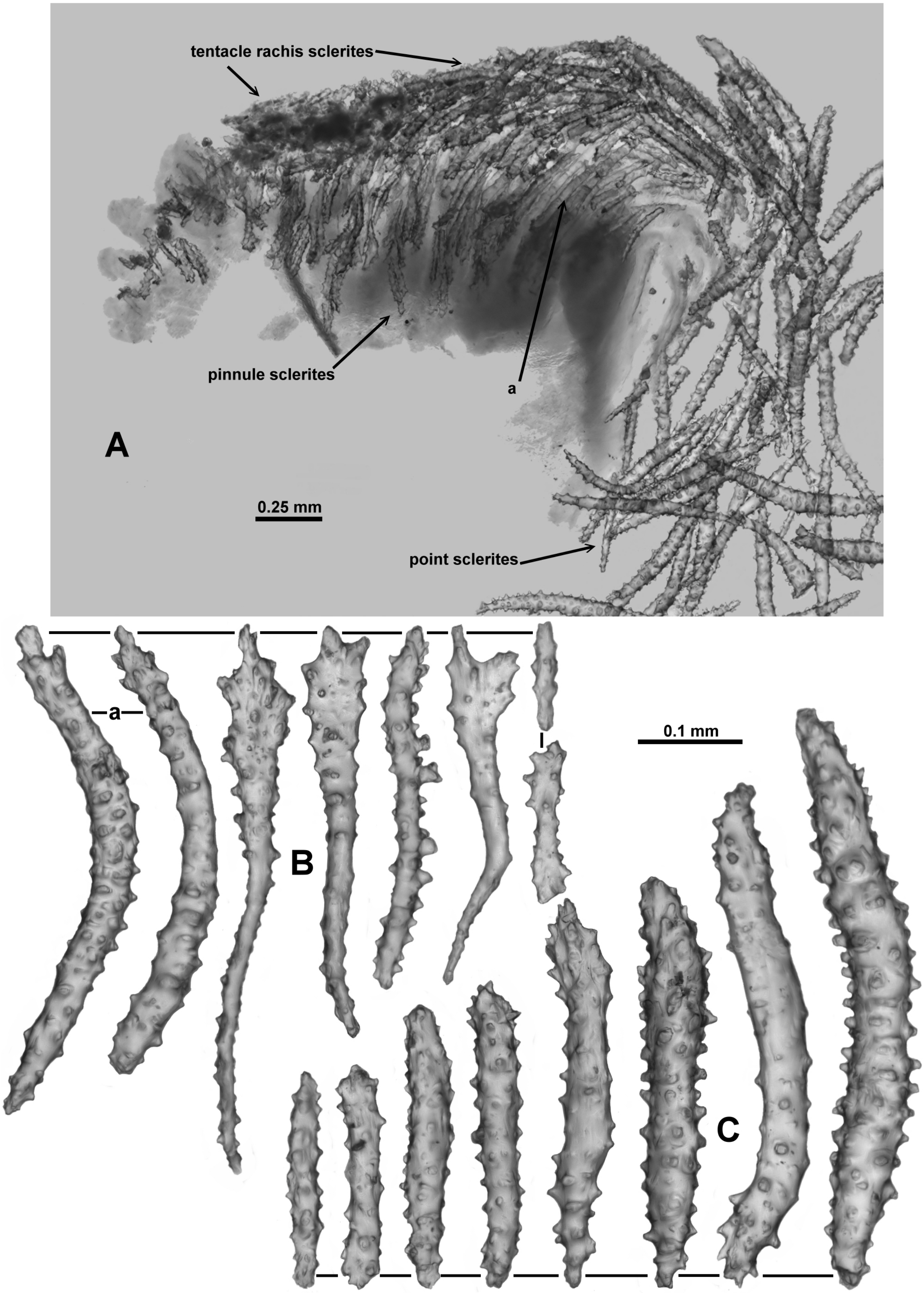

Figure 2.26. *Anthothela vickersi* (Benham, 1928): A. TMAG K4264, tentacle and point sclerites in situ (a. spatulate clubs). B-C. TMAG K3985, sclerites: (B). Pinnule (a. long sticks); (C). Tentacle rachis.

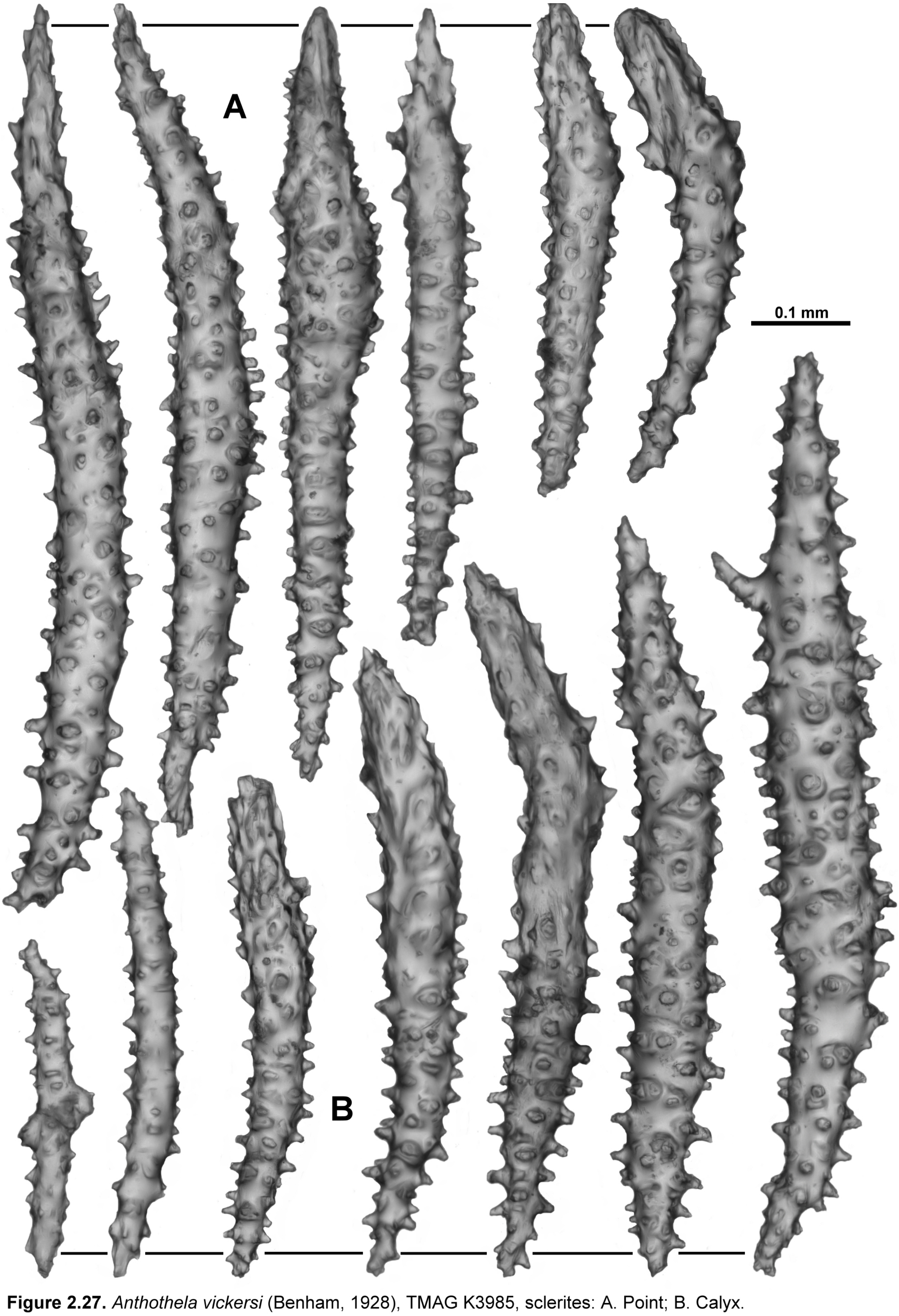

Figure 2.27. *Anthothela vickersi* (Benham, 1928), TMAG K3985, sclerites: A. Point; B. Calyx.

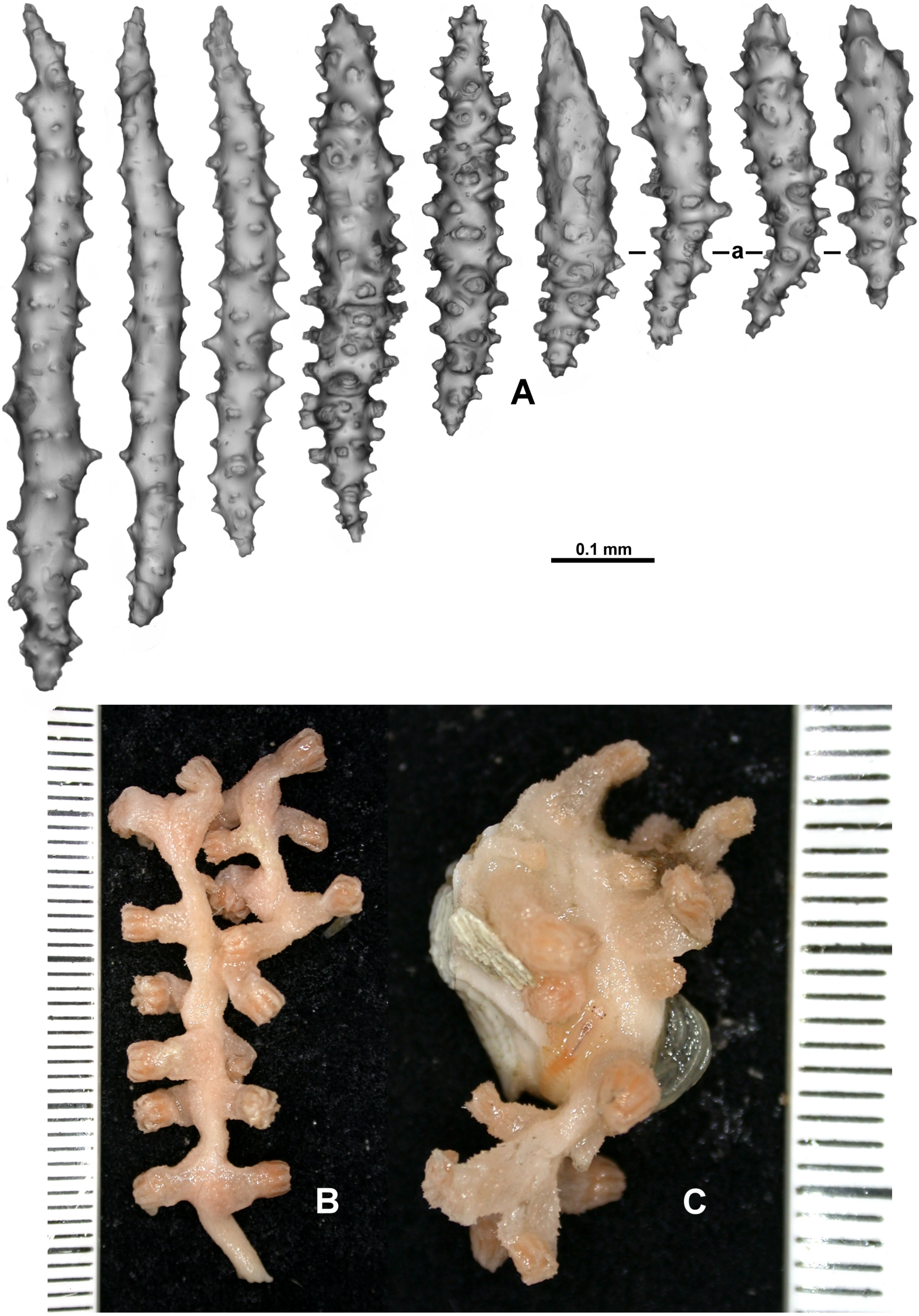

Figure 2.28. *Anthothela vickersi* (Benham, 1928): A. TMAG K3985, cortex sclerites (a. small clubs); B. TMAG K3984, recently collected specimen; C. TMAG K3985, recently collected specimen. (B-C. Courtesy of Karen Gowlett-Holmes, CMAR).

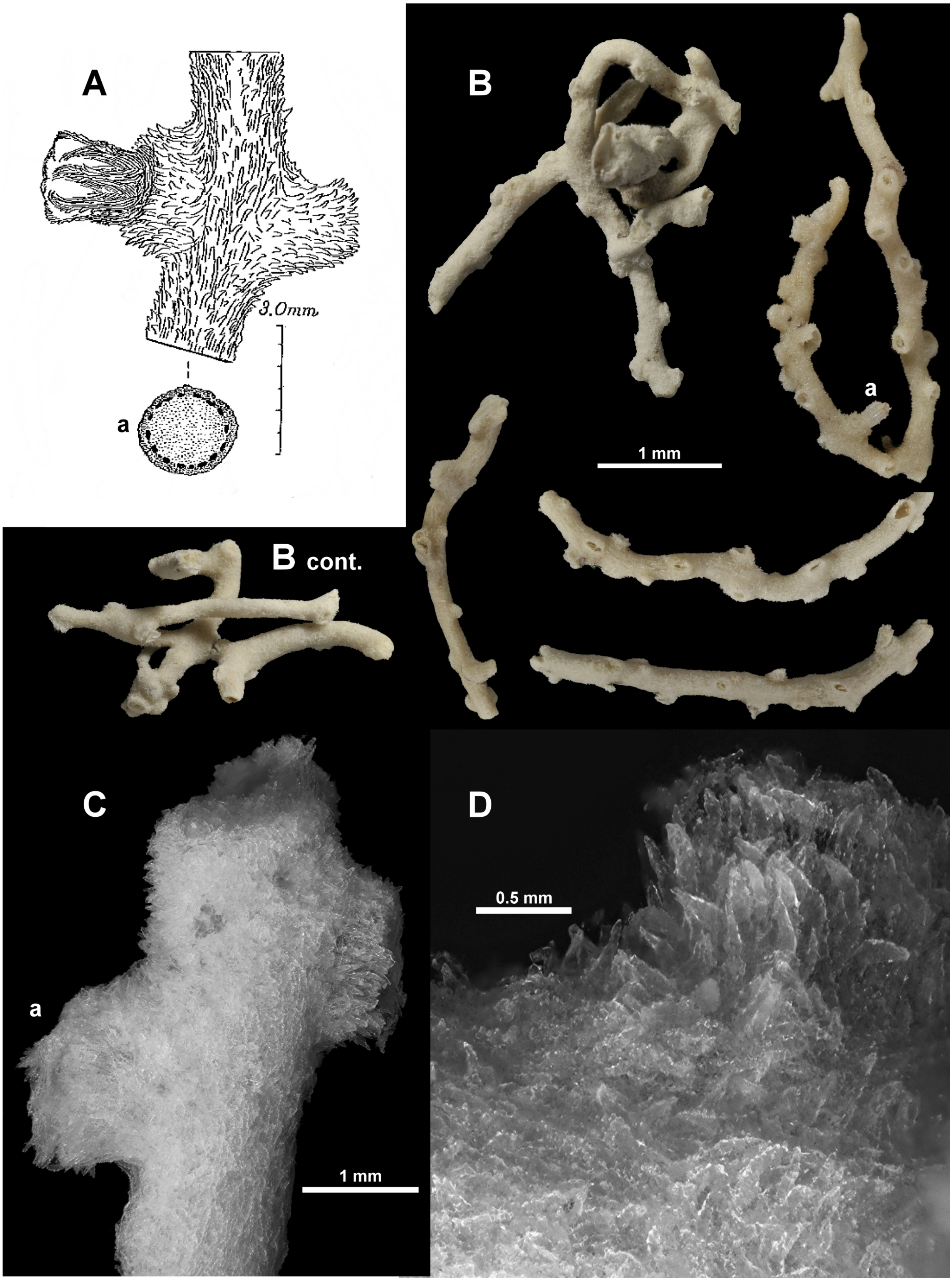

Figure 2.29. *Anthothela tropicalis,* Bayer, 1961, holotype: A. Colony diagram from Bayer 1961, Fig. 13g; B. Colony fragments; C. Fragment examined (a. small retracted polyp); D. Sclerites projecting out from a calyx and cortex. (B. Courtesy of NMNH, Dr R. Ford).

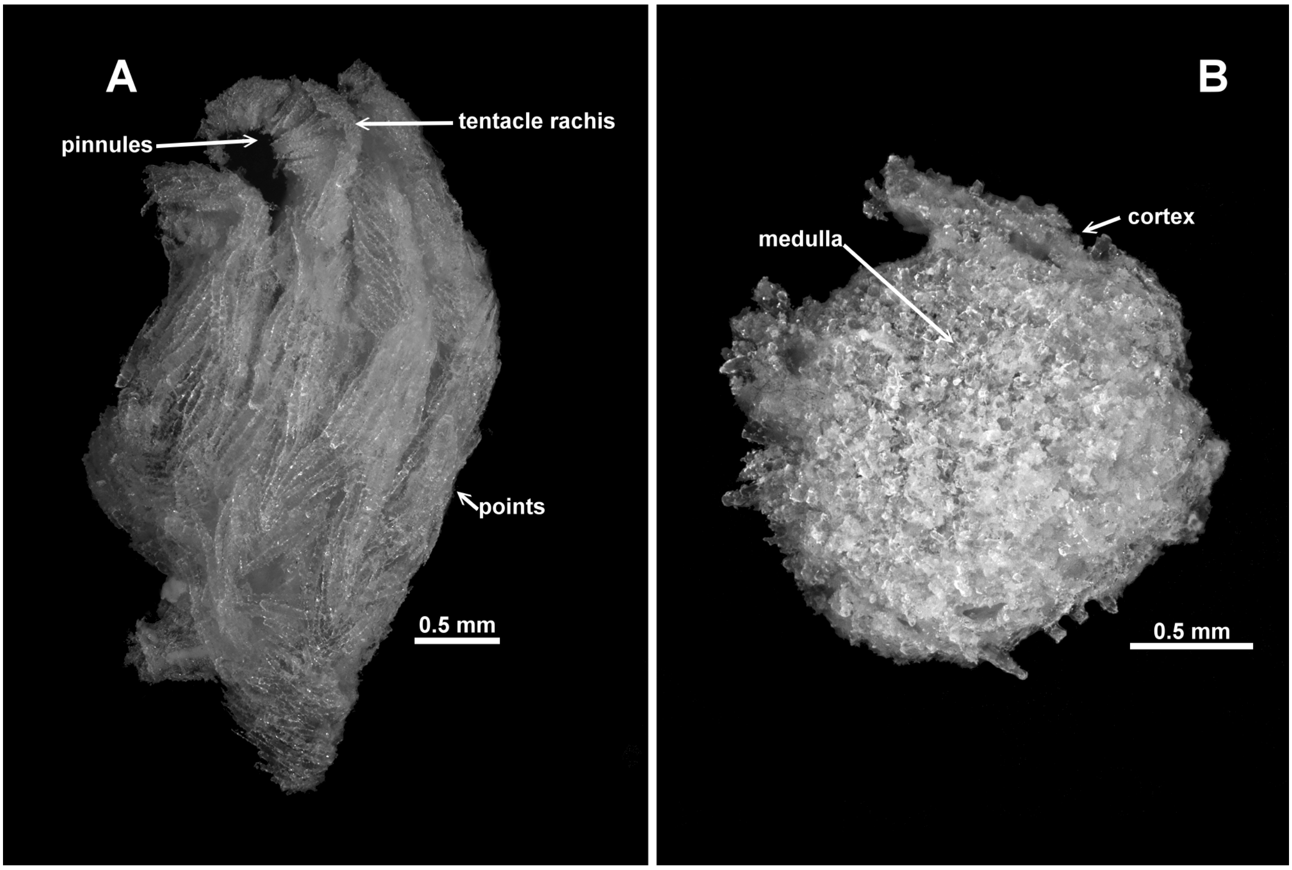

Figure 2.30. *Anthothela tropicalis* Bayer, 1961, holotype: A. Fragment of polyp head showing points, collaret, tentacle rachis and pinnules; B. Cross-section of medulla.

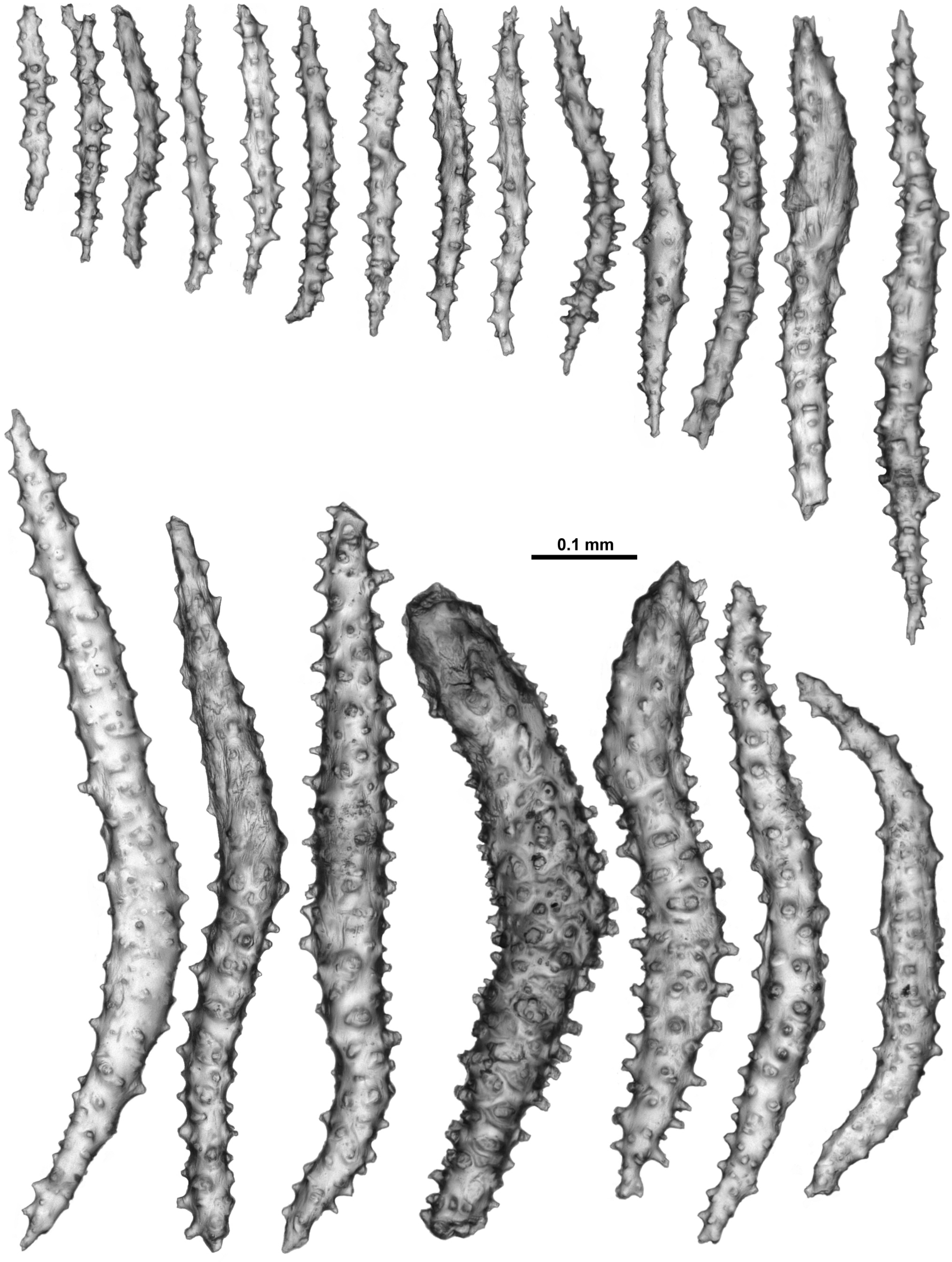

Figure 2.31. *Anthothela tropicalis*, Bayer, 1961, holotype, sclerites: Point and collaret.

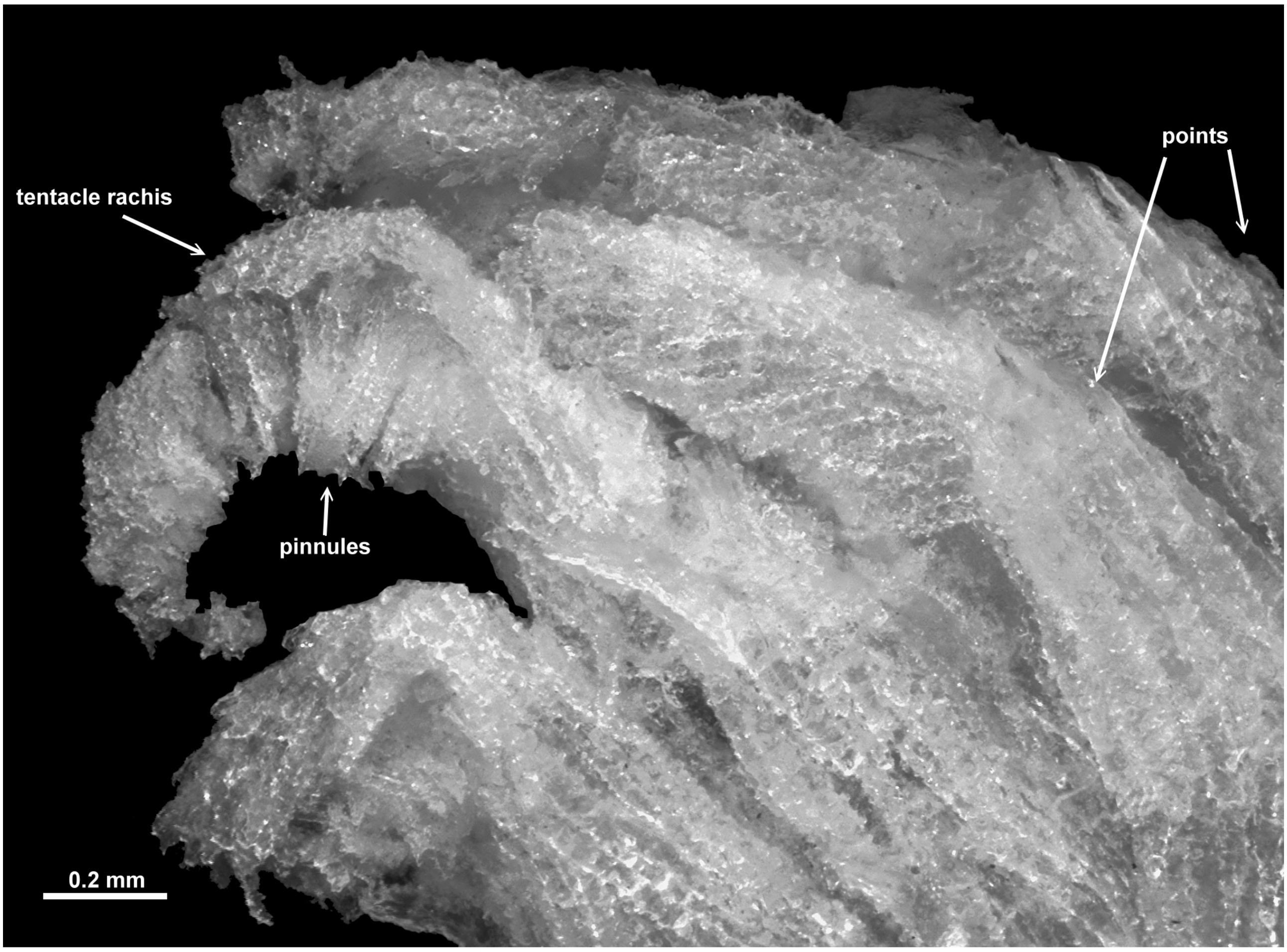

Figure 2.32. *Anthothela tropicalis*, Bayer, 1961, holotype: Arrangement of sclerties in the points, tentacle rachis and pinnules.

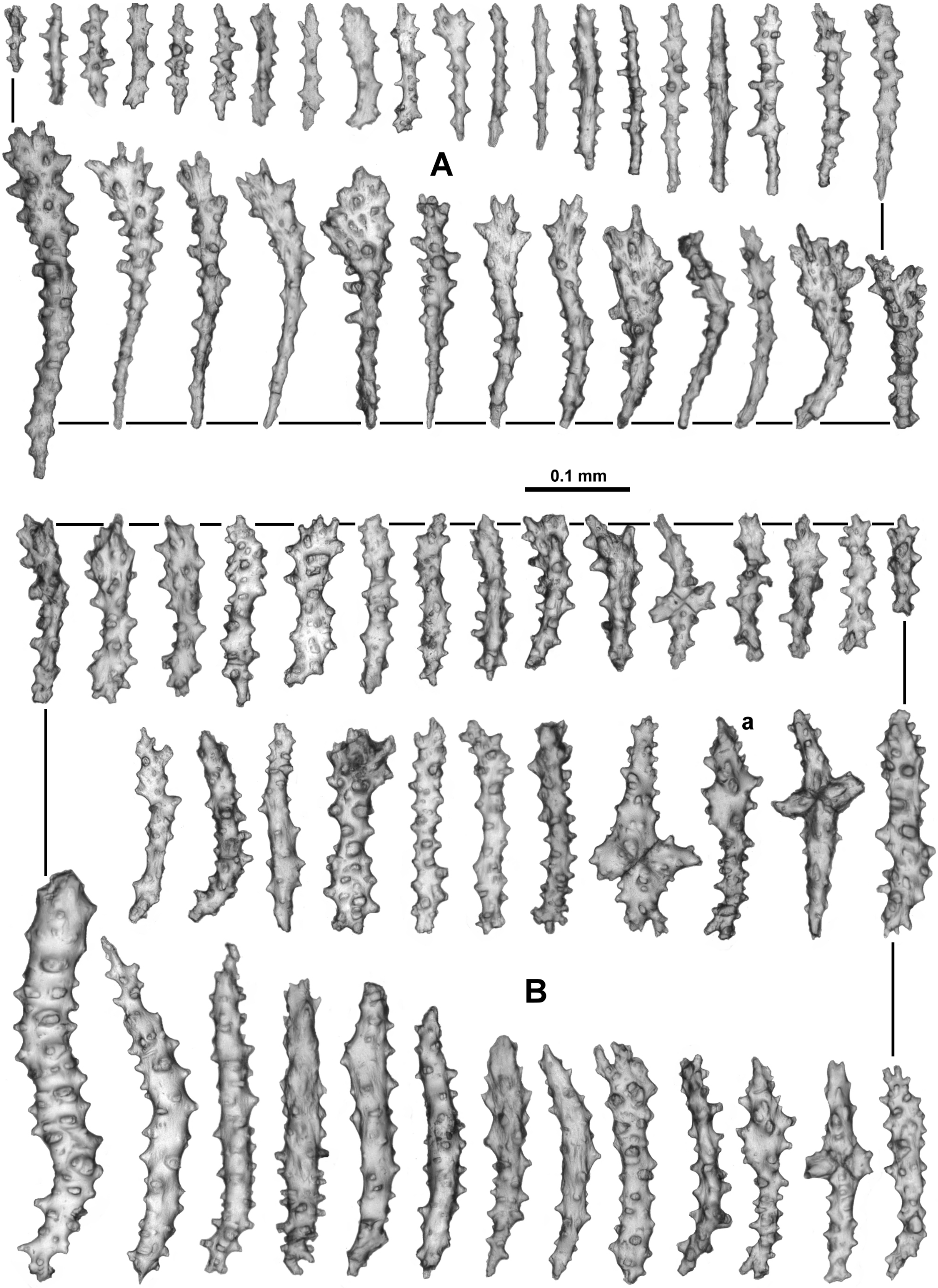

Figure 2.33. *Anthothela tropicalis*, Bayer, 1961, holotype, sclerites: A. Pinnule; B. Tentacle rachis (a. short, clavate spindle as mentioned by Bayer 1961).

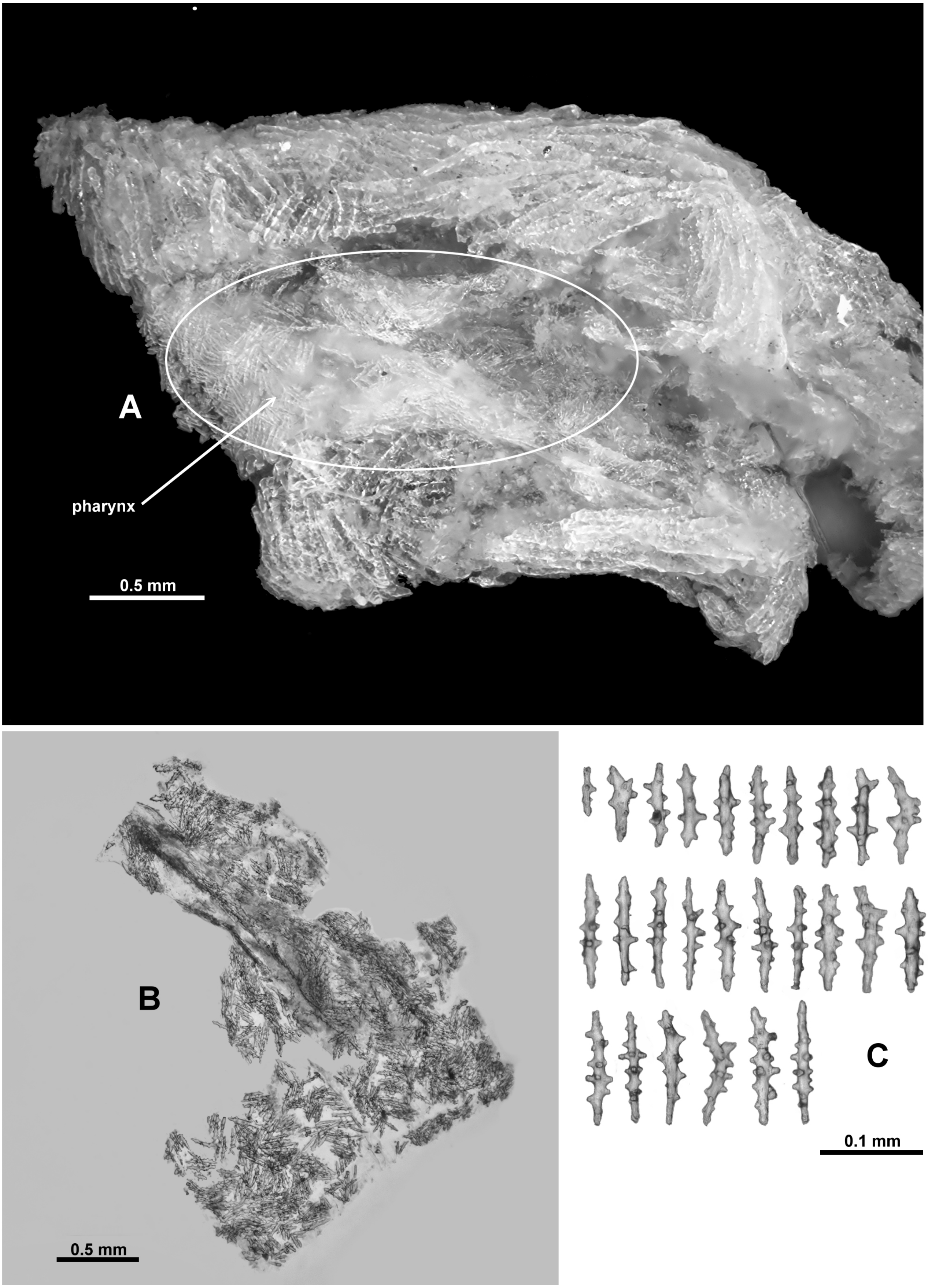

Figure 2.34. *Anthothela tropicalis*, Bayer,1961, holotype: A. Polyp head with pharynx in place; B. In situ arrangement of pharynx sclerites; C. Pharynx sclerites.

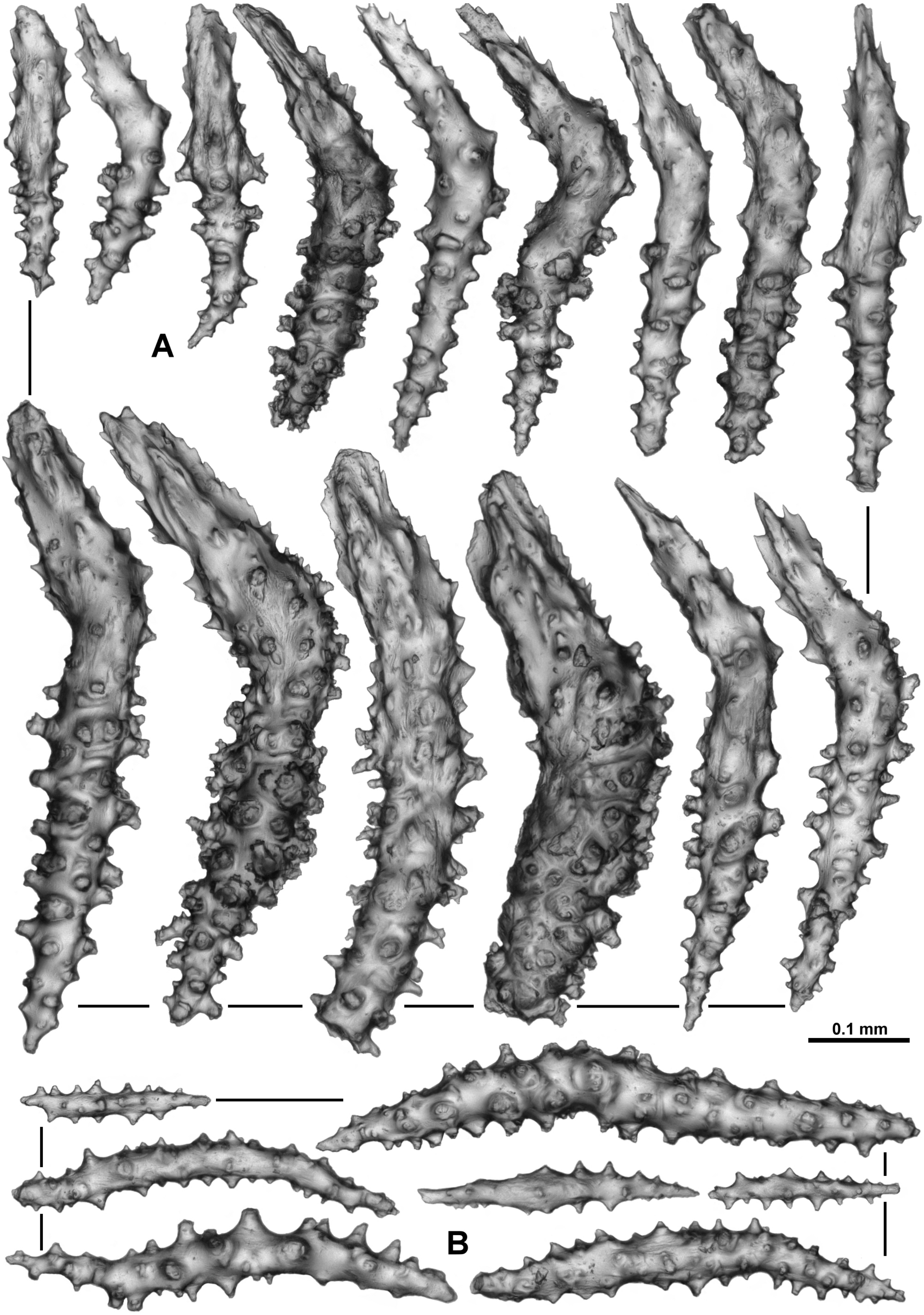

Figure 2.35. *Anthothela tropicalis*, Bayer, 1961, holotype, calyx sclerites: A. Thorn clubs; B. Spindles and sticks.

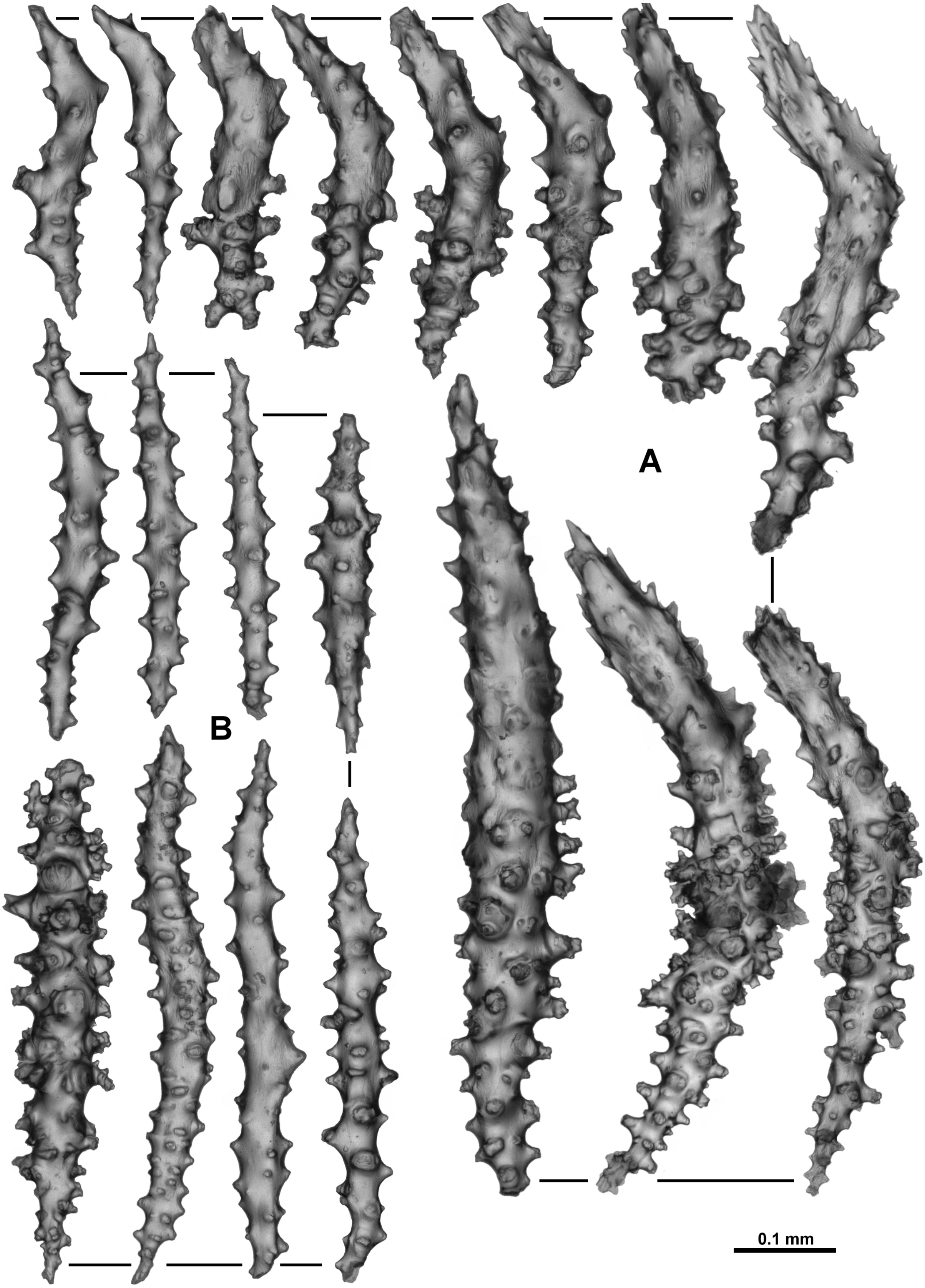

Figure 2.36. *Anthothela tropicalis*, Bayer, 1961, holotype, cortex sclerites: A. Thorn clubs; B. Spindles and sticks.

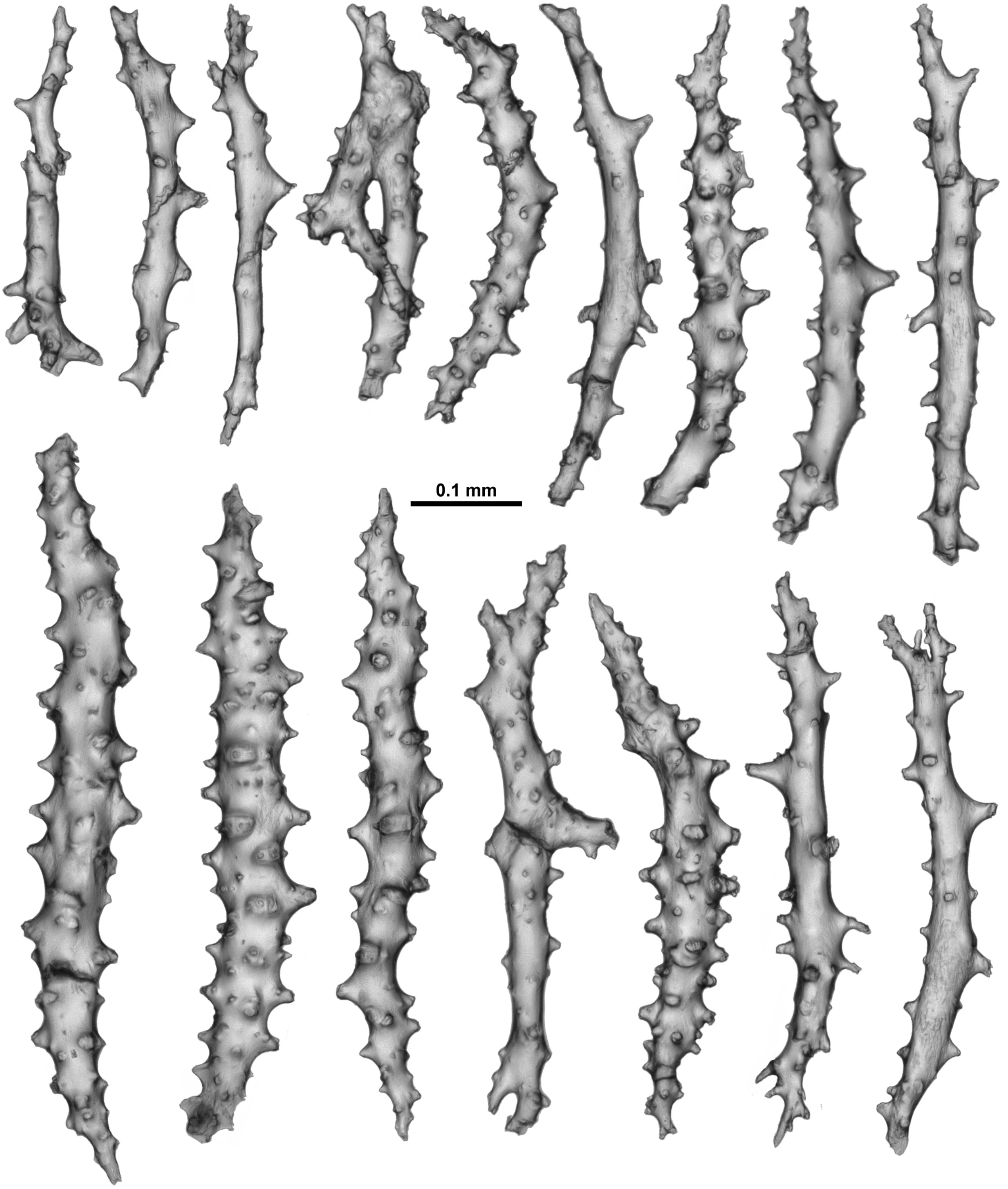

Figure 2.37. *Anthothela tropicalis*, Bayer, 1961, holotype, sclerites: Medulla.

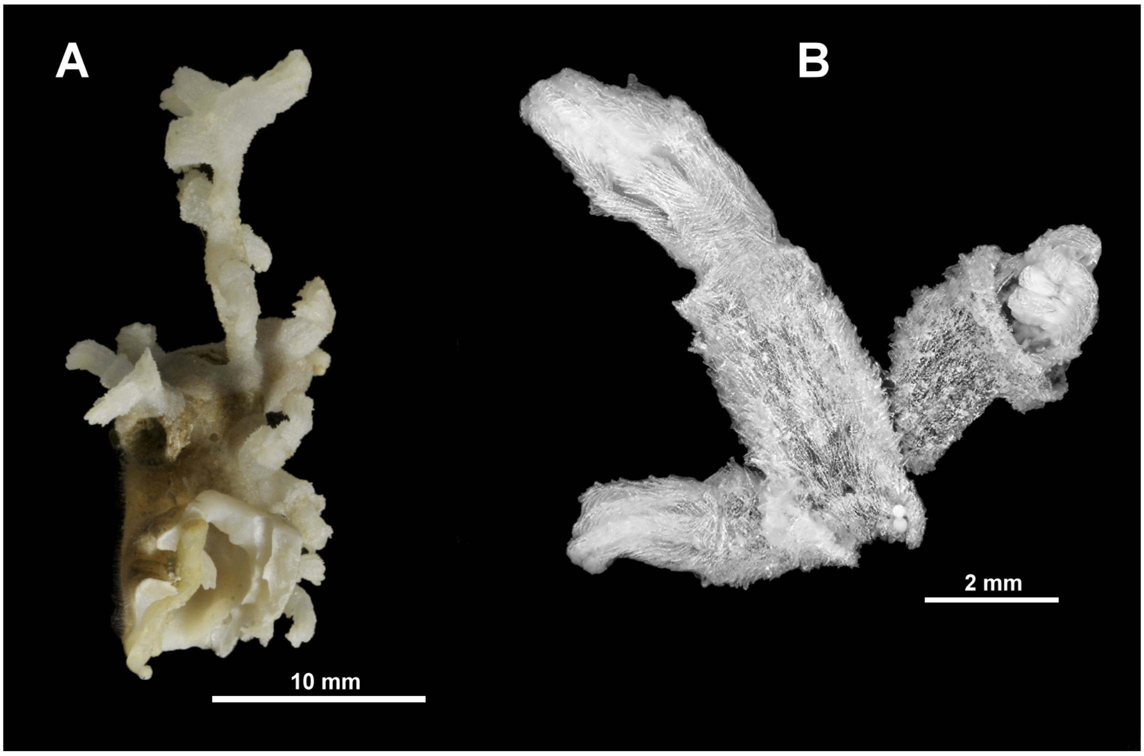

Figure 2.38. *Anthothela tropicalis*, USNM 1090549: A. Colony; B. Terminal polyp bunch.

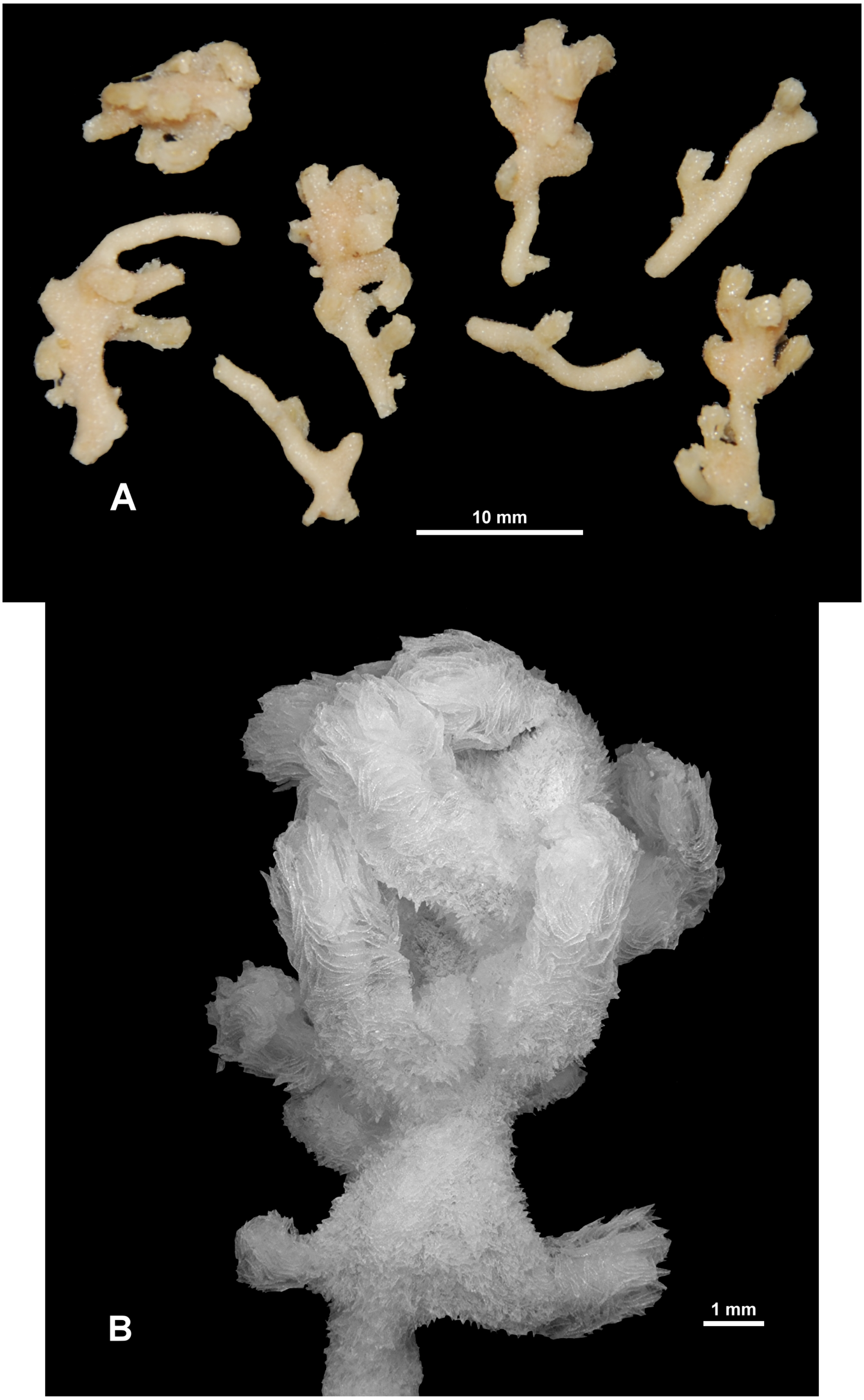

Figure 2.39. *Anthothela aldersladei* n. sp., holotype: A. Colony fragments; B. Polyp bunch.

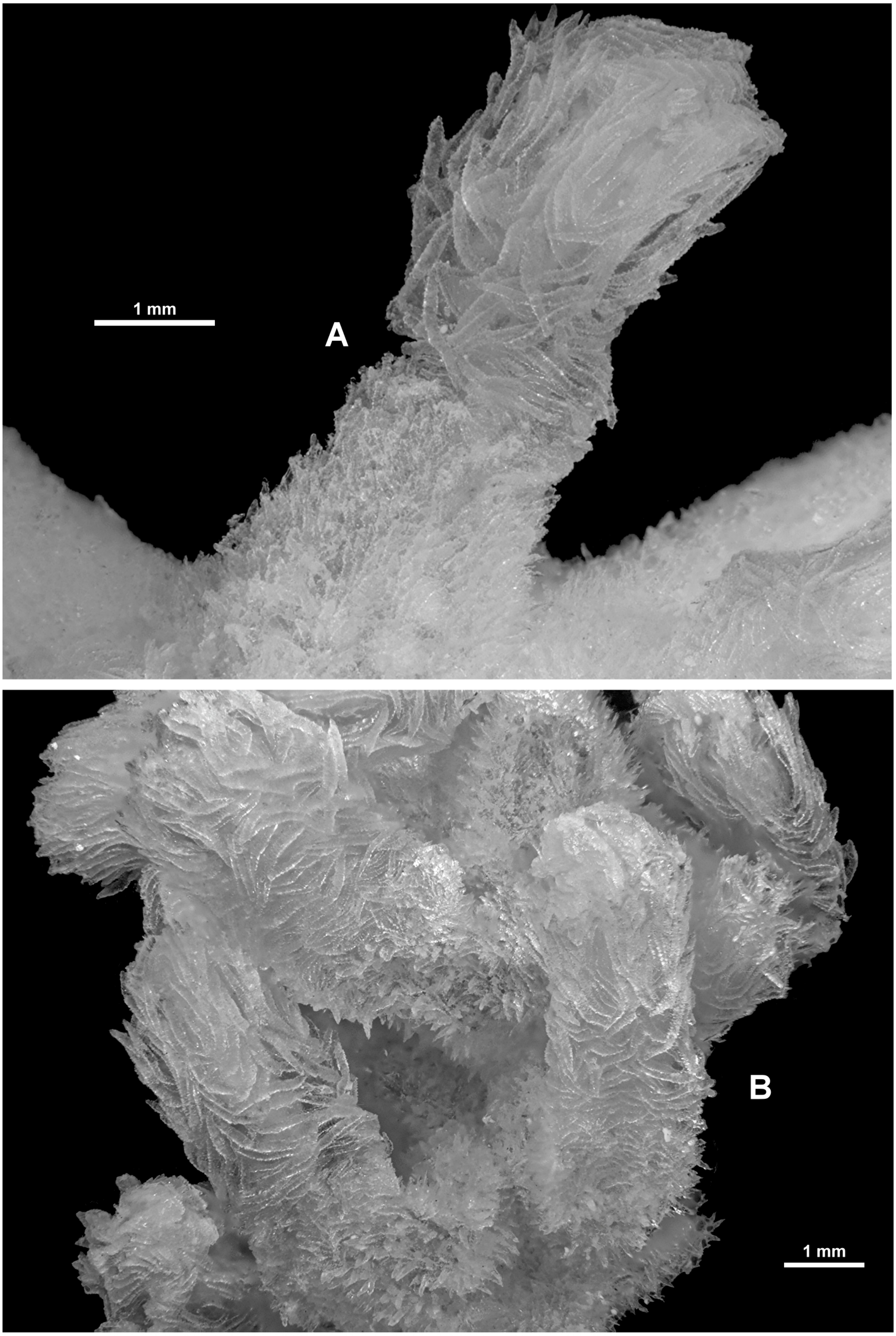

Figure 2.40. *Anthothela aldersladei*, n. sp., holotype: A. Extended polyp; B. Polyp bunch.

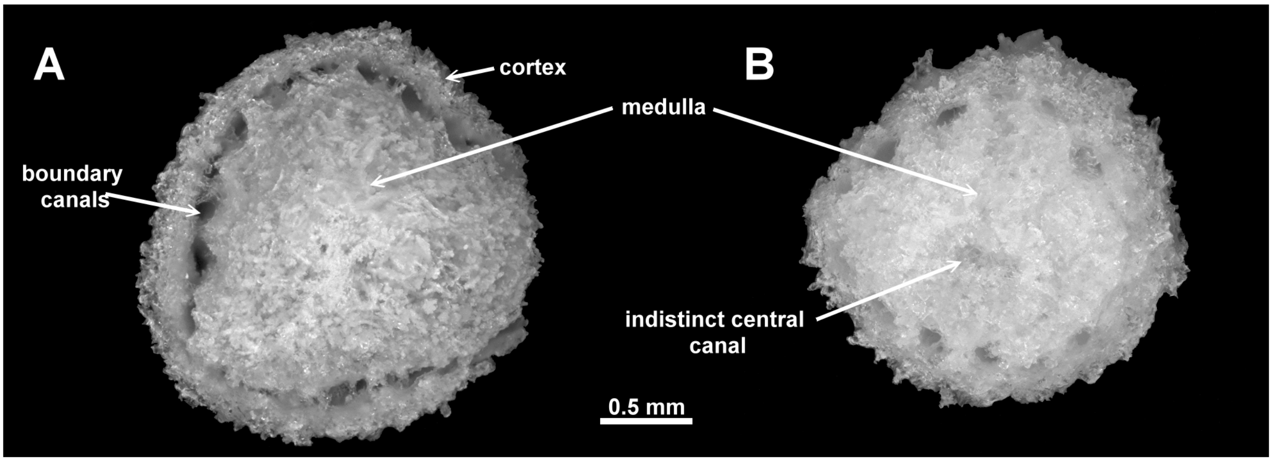

Figure 2.41. *Anthothela aldersladei,* n. sp., holotype: A-B. Cross-section of medulla.

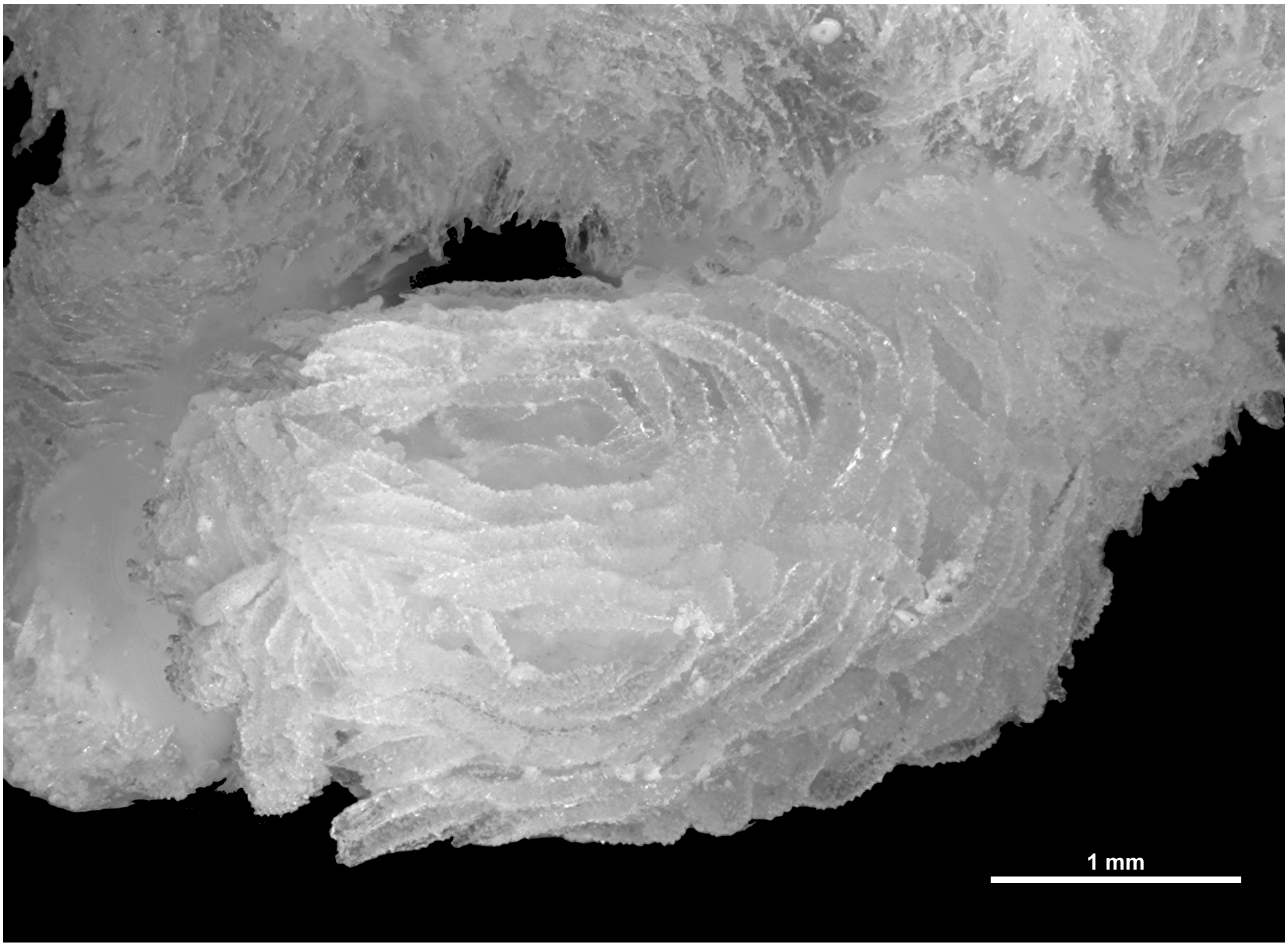

Figure 2.42. *Anthothela aldersladei*, n. sp., holotype: Arrangement of sclerites in points and on polyp neck.

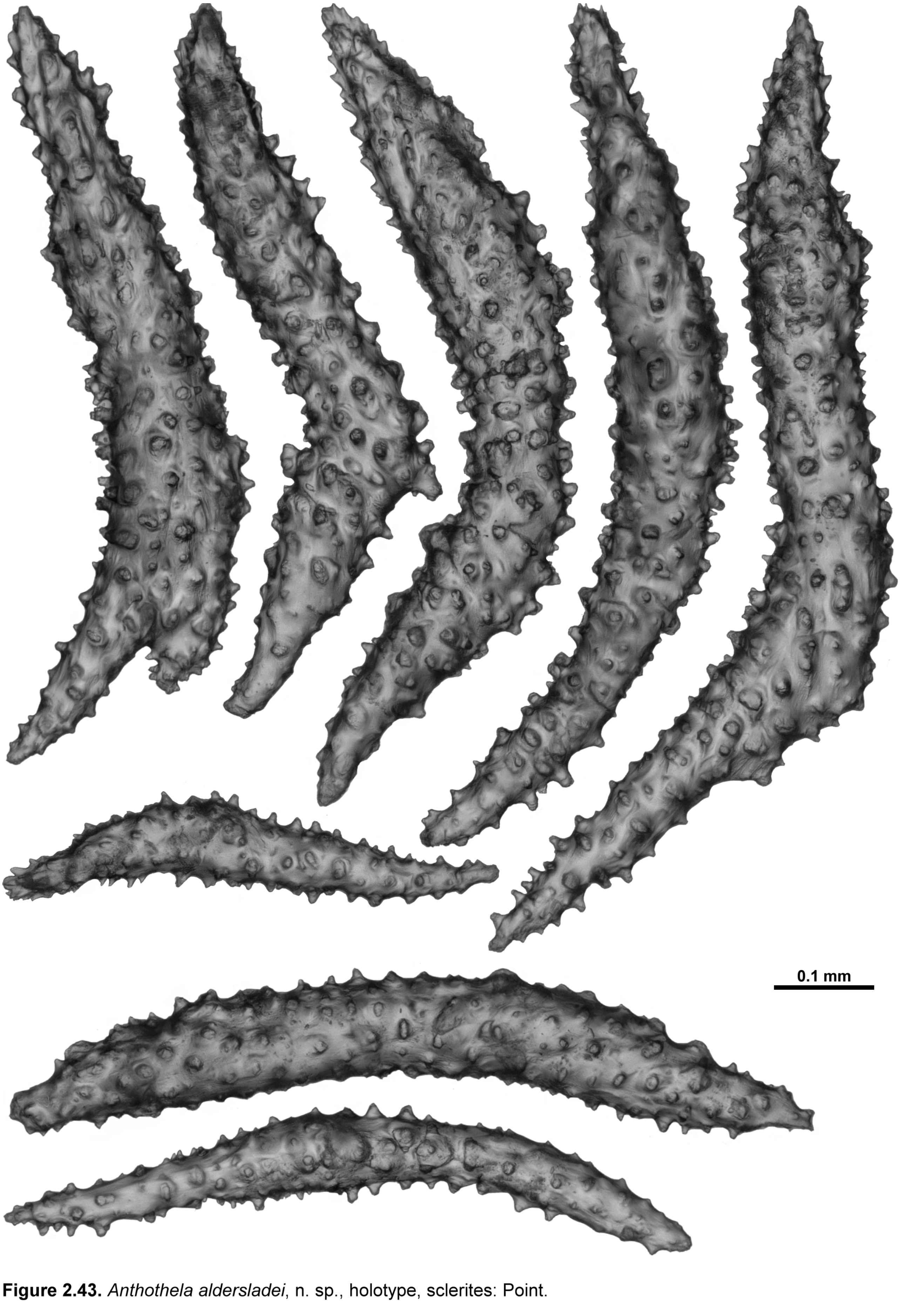

Figure 2.43. *Anthothela aldersladei*, n. sp., holotype, sclerites: Point.

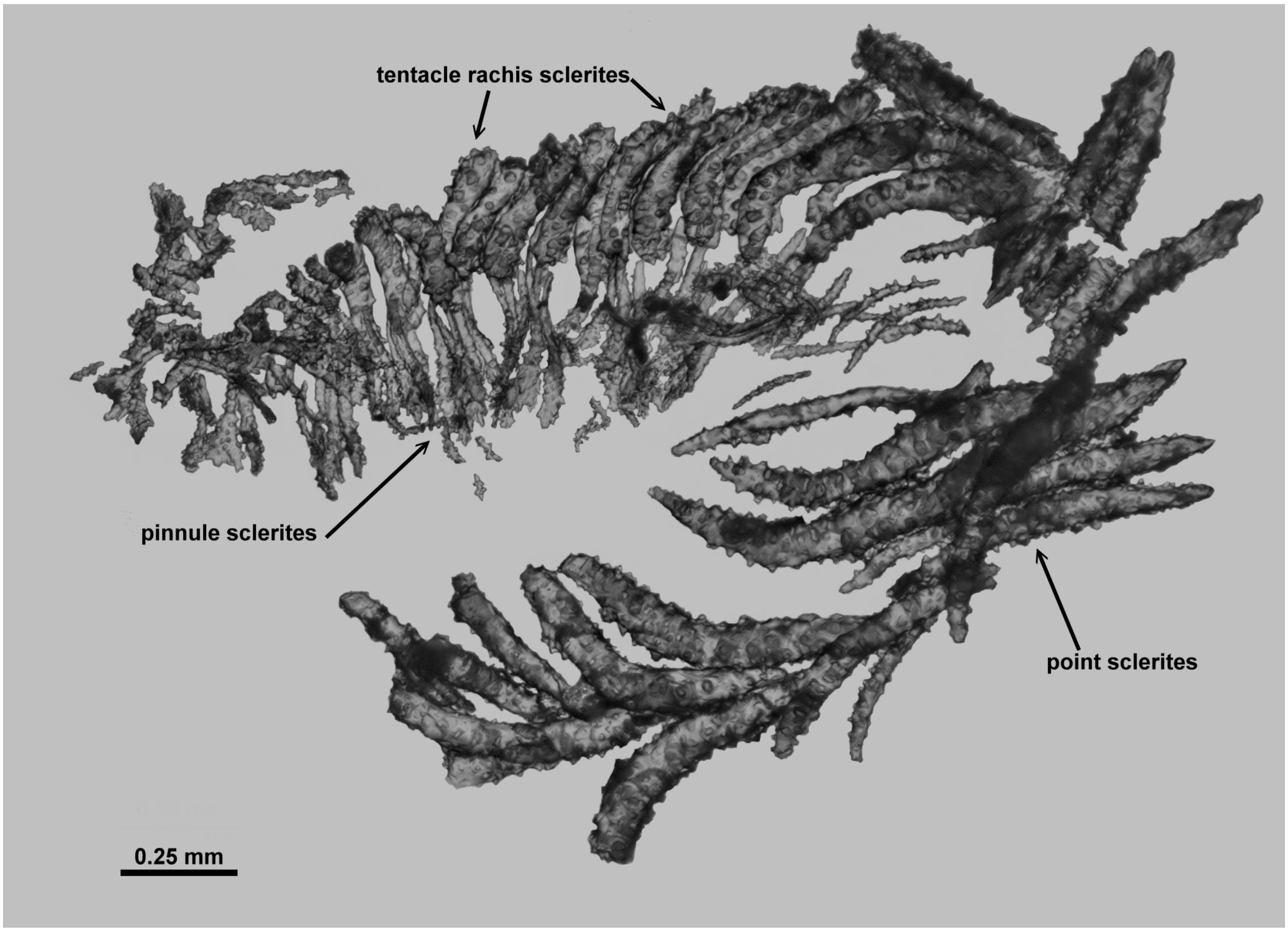

Figure 2.44. *Anthothela aldersladei*, n. sp., holotype: Tentacle and point sclerites in situ.

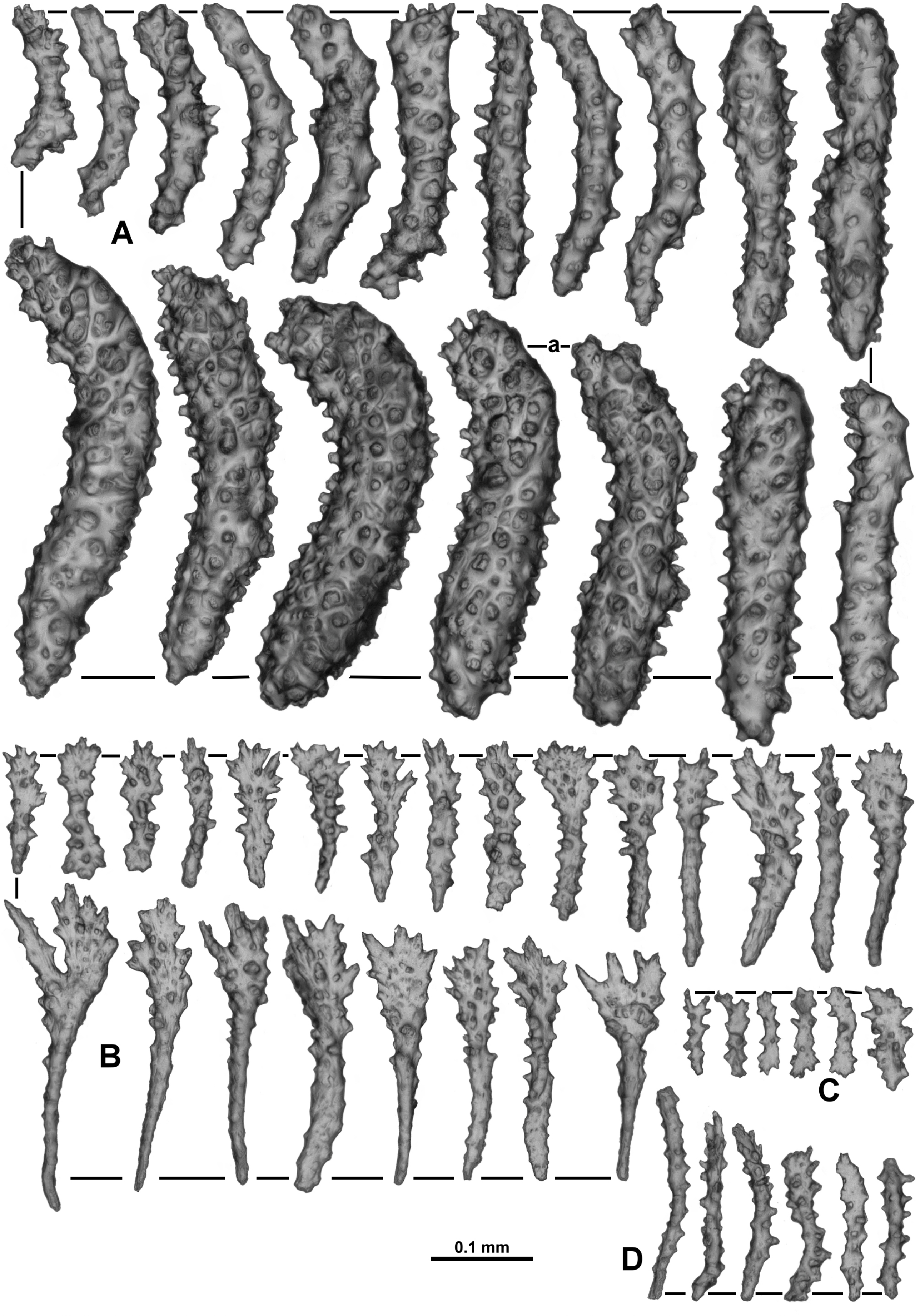

Figure 2.45. *Anthothela aldersladei*, n. sp., holotype, sclerites: A. Tentacle rachis (a. sclerites with one curved tip) B-D. Pinnules.

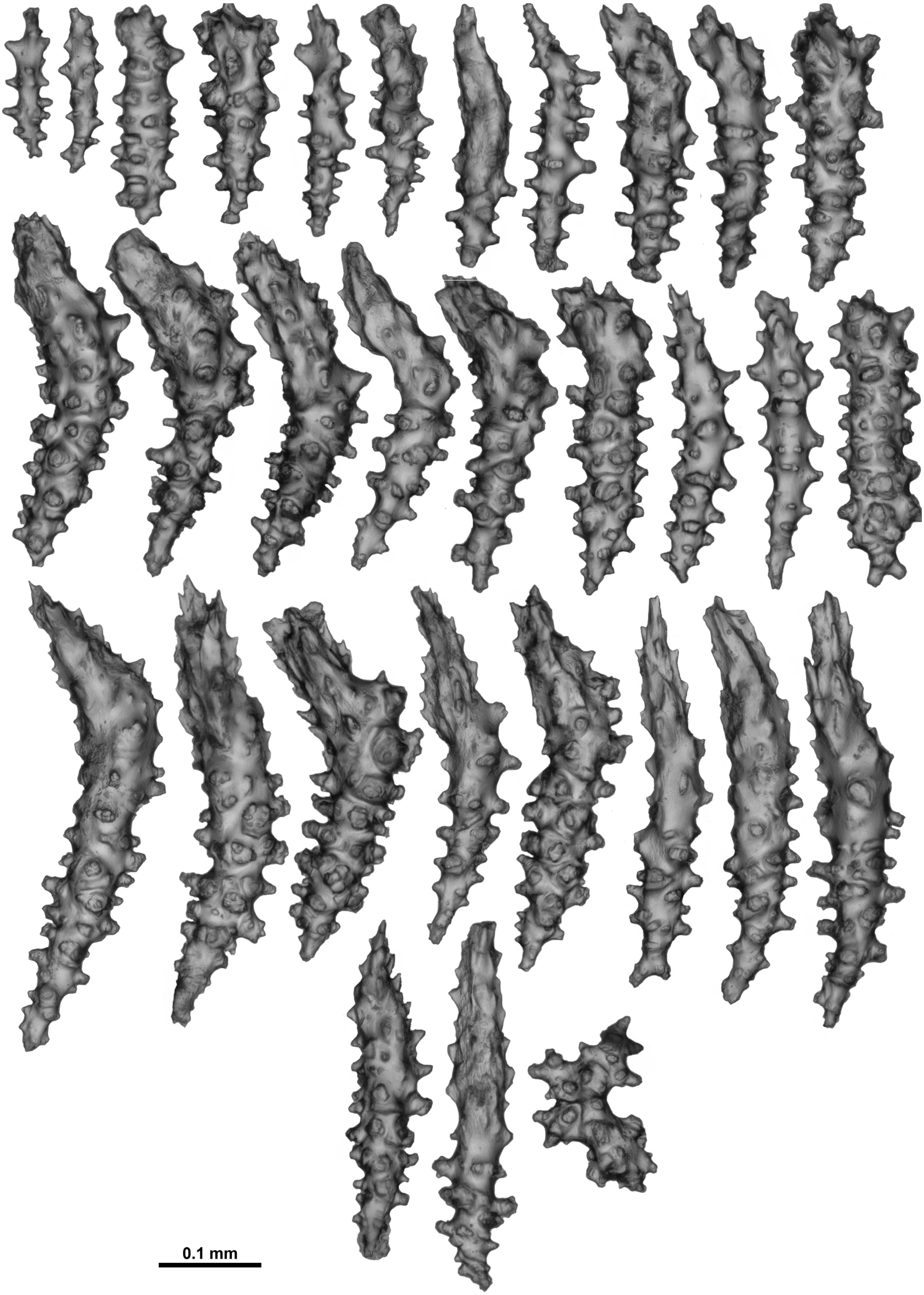

Figure 2.46. *Anthothela aldersladei,* n. sp., holotype, sclerites: Calyx.

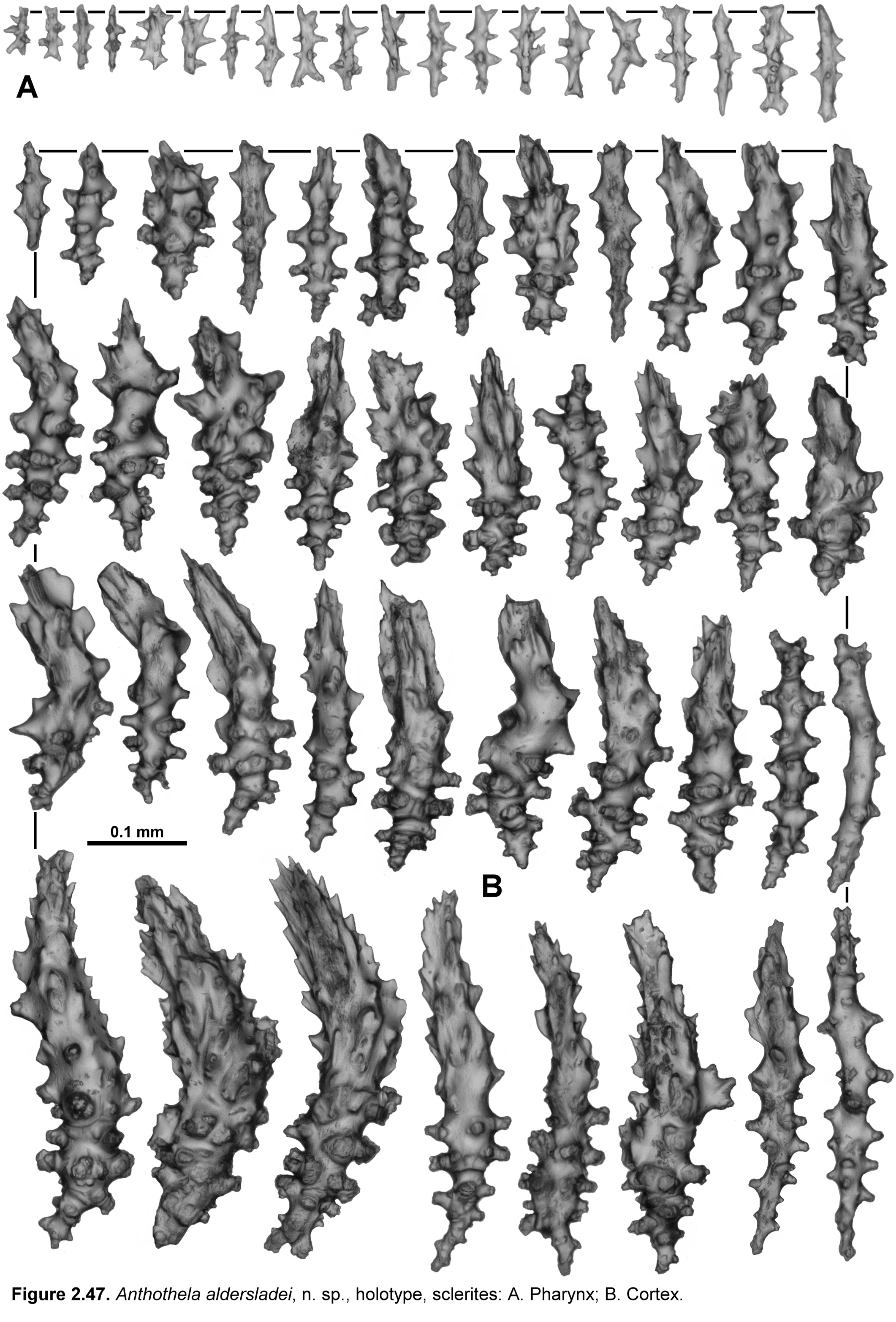

Figure 2.47. *Anthothela aldersladei*, n. sp., holotype, sclerites: A. Pharynx; B. Cortex.

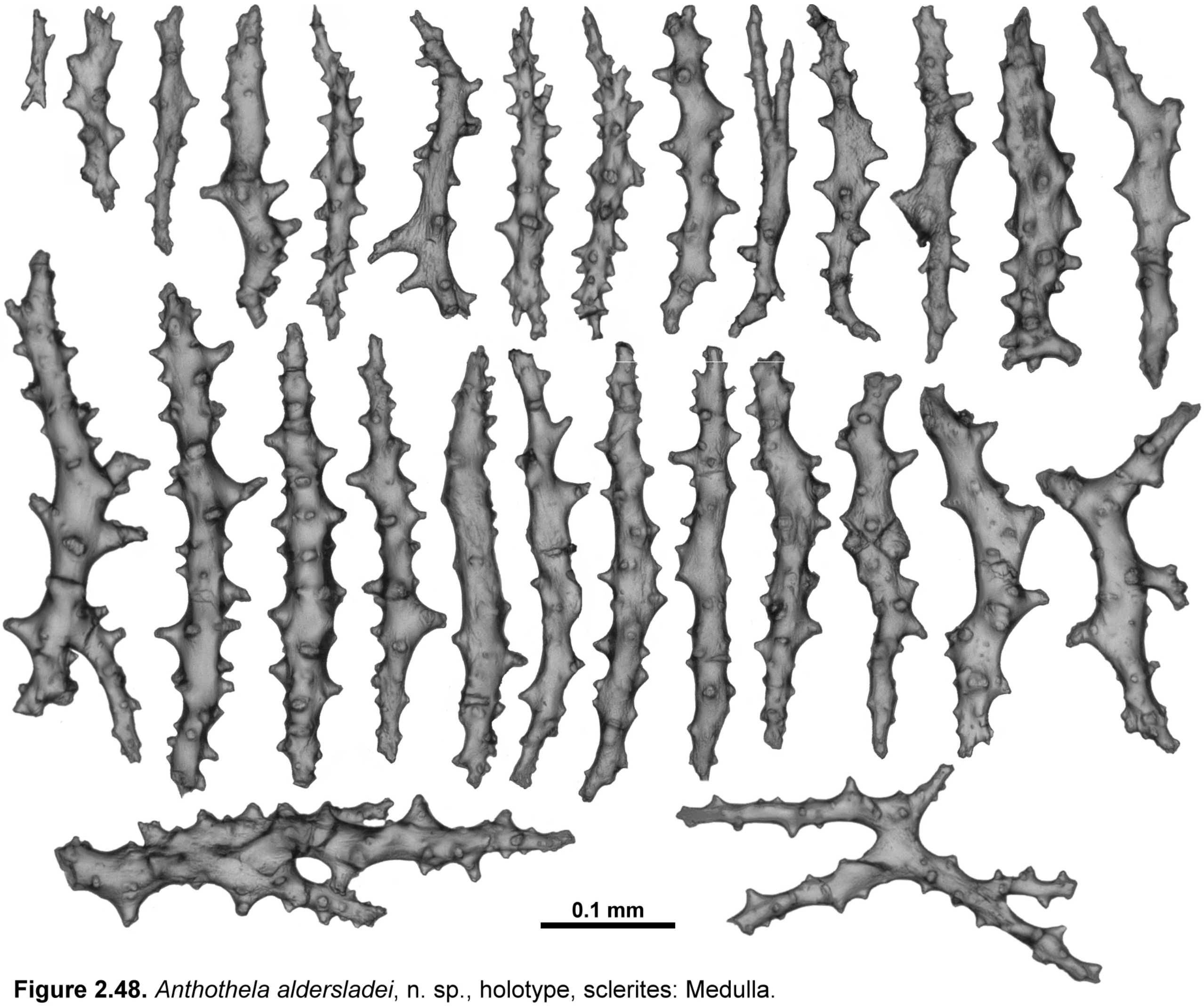

Figure 2.48. *Anthothela aldersladei*, n. sp., holotype, sclerites: Medulla.

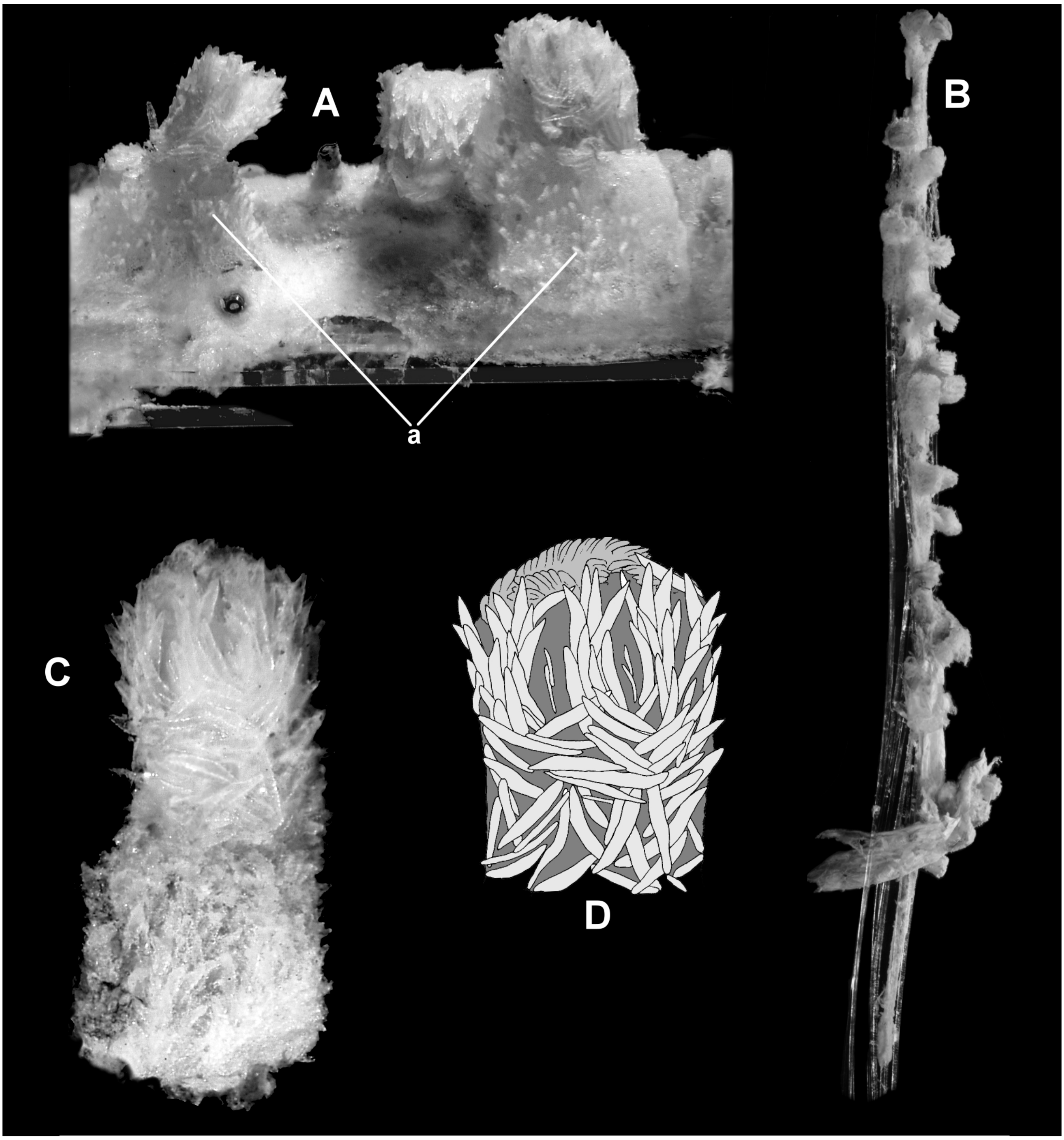

Figure 2.49. *Anthothela aldersladei* n. sp., WAM Z13059: A. Portion of colony (a. projecting sclerites on calyces); B. Entire colony growing on sponge spicules; C. Extended polyp; D. Polyp head with points arrangment. (A-D. Courtesy of Dr. P. Alderslade).

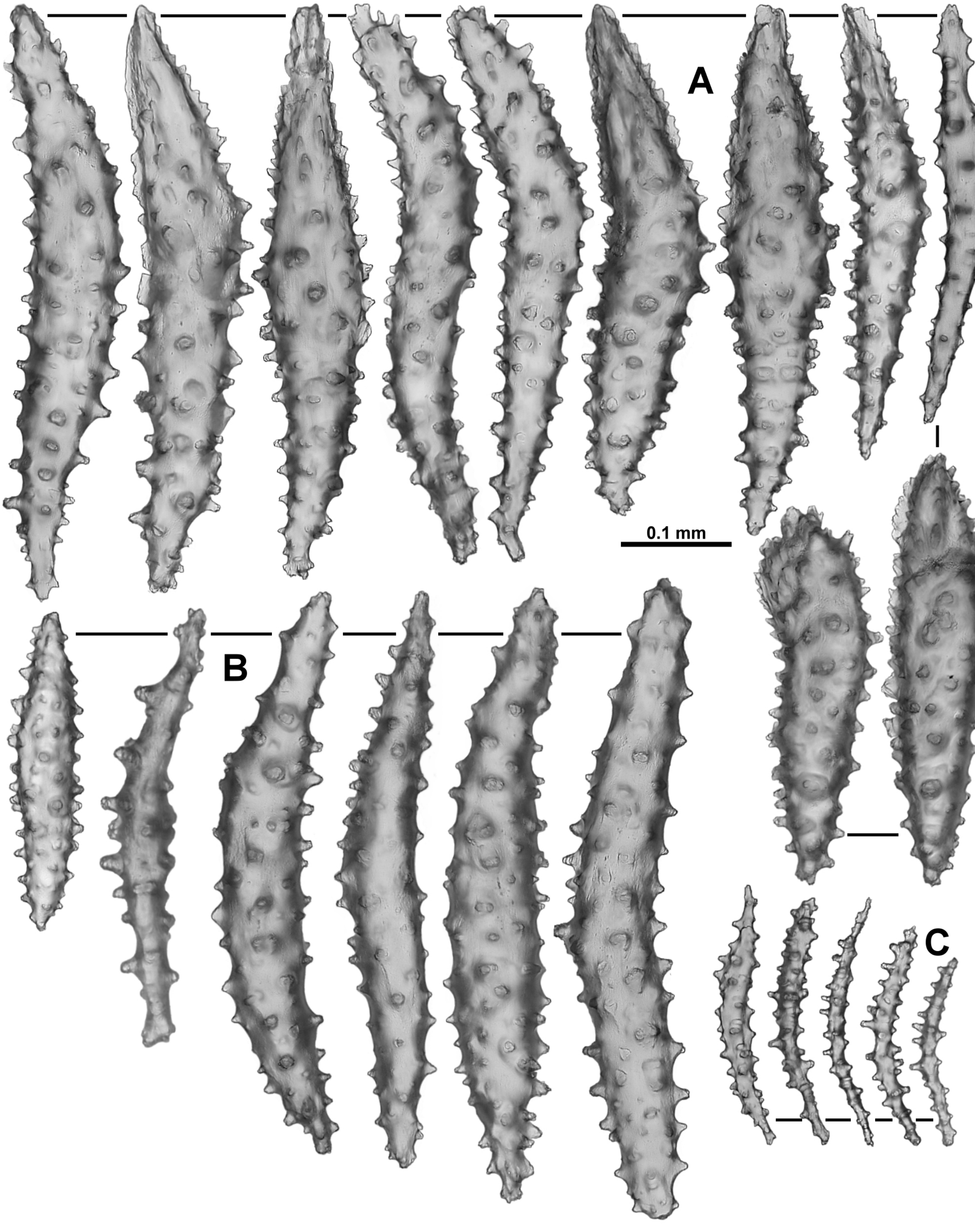

Figure 2.50. *Anthothela aldersladei* n. sp., WAM Z13059, sclerites: A. Point; B. Neck; C. Intermediate. (A-C. Courtesy of Dr. P. Alderslade).

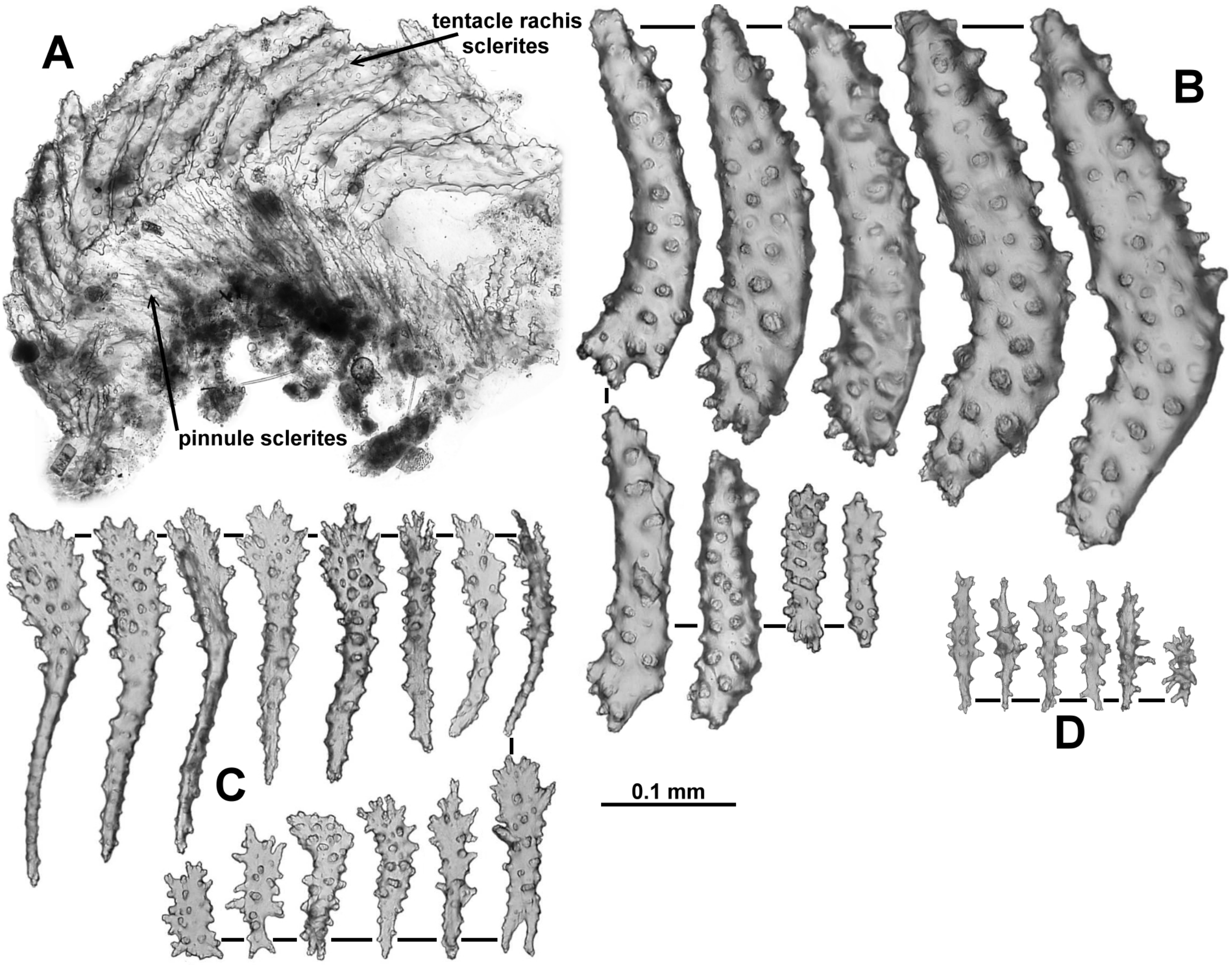

Figure 2.51. *Anthothela aldersladei* n. sp., WAM Z13059: A. Tentacle sclerites in situ; B. Tentacle rachis sclerites C. Pinnule sclerites; D. Pharynx sclerites. (A-D. Courtesy of Dr P. Alderslade).

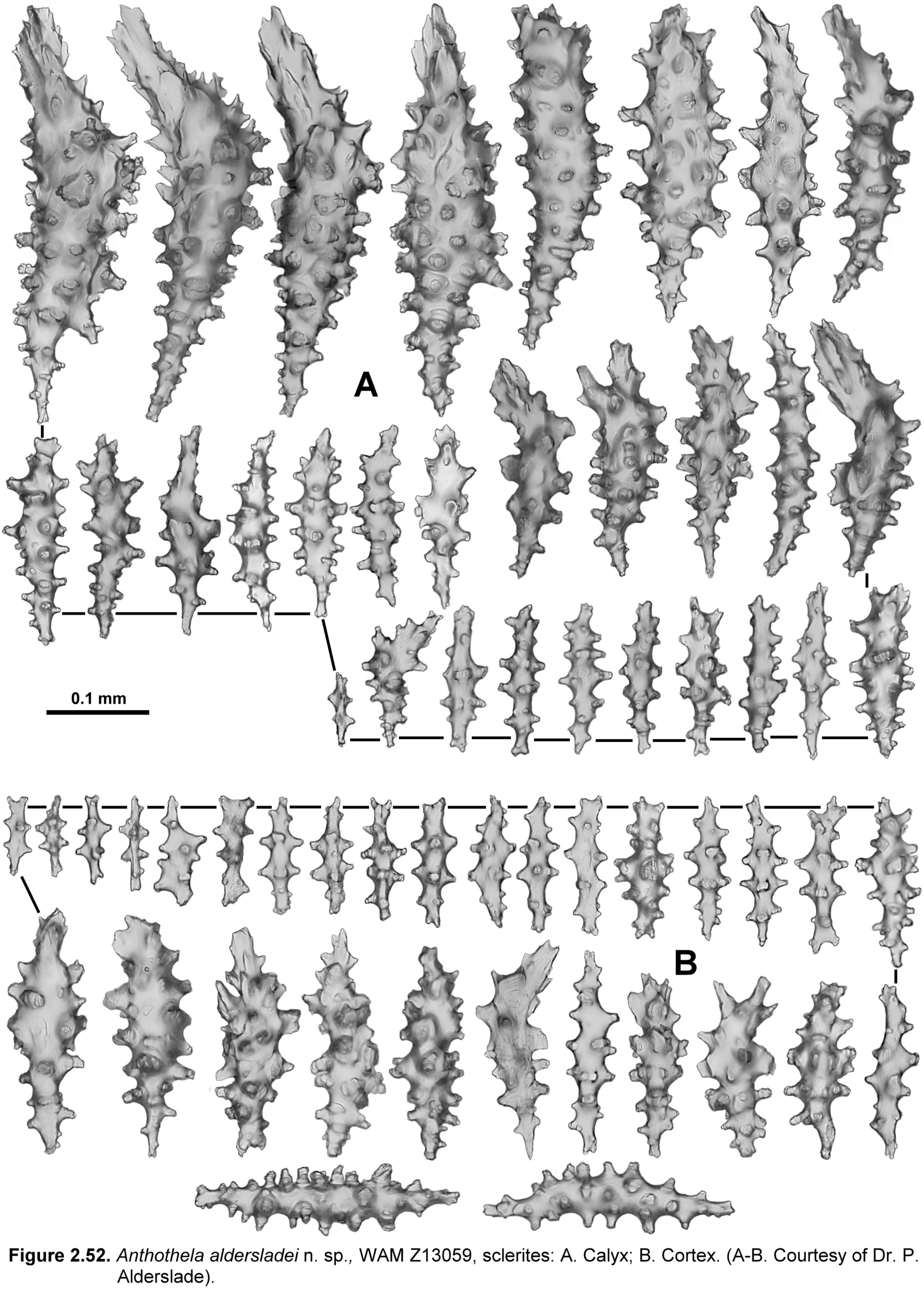

Figure 2.52. *Anthothela aldersladei* n. sp., WAM Z13059, sclerites: A. Calyx; B. Cortex. (A-B. Courtesy of Dr. P. Alderslade).

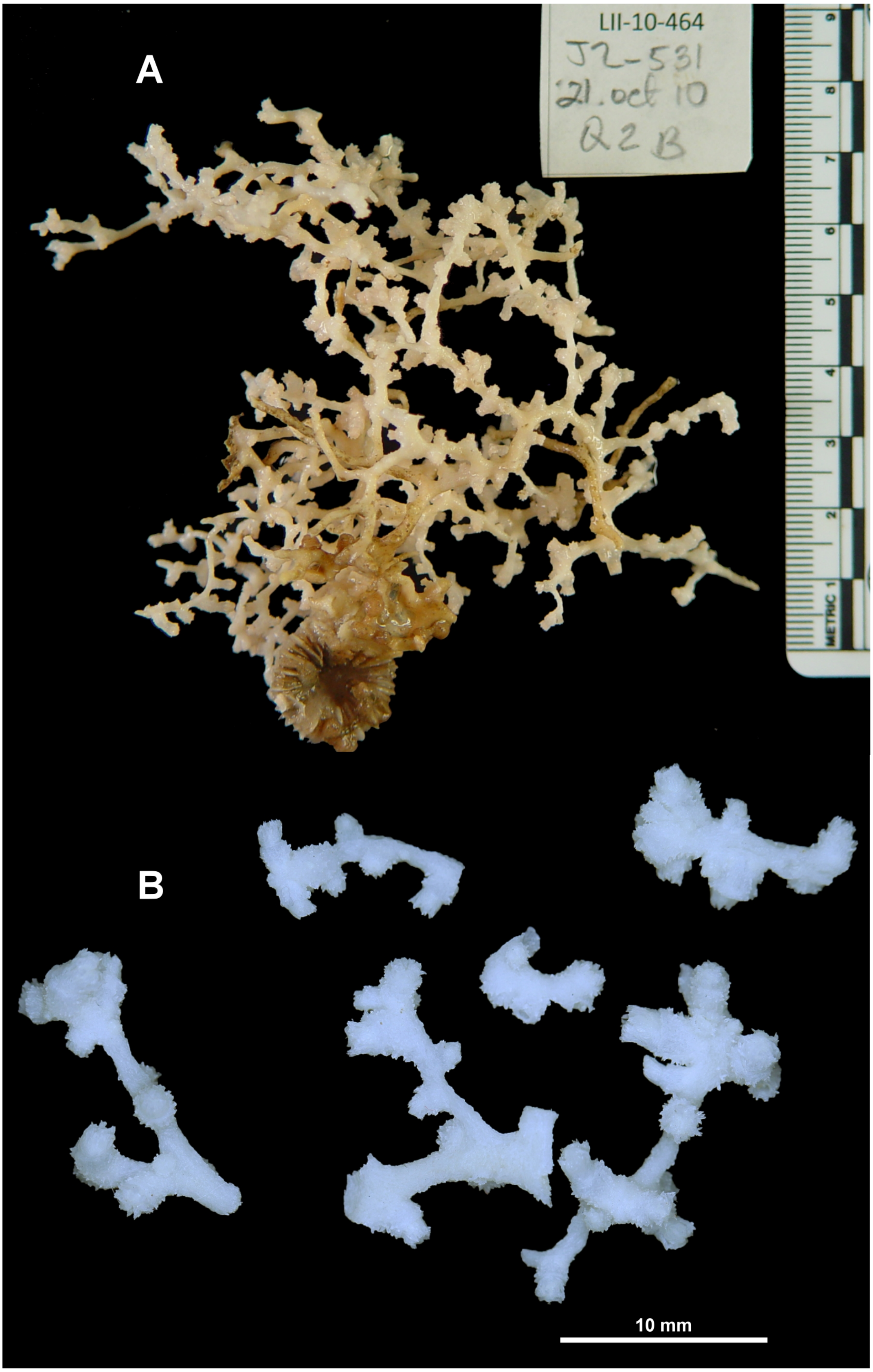

Figure 2.53. *Anthothela quattriniae,* n. sp., holotype: A. Colony; B. Fragments examined. (A. Courtesy of the Lophelia II 2010 Expedition).

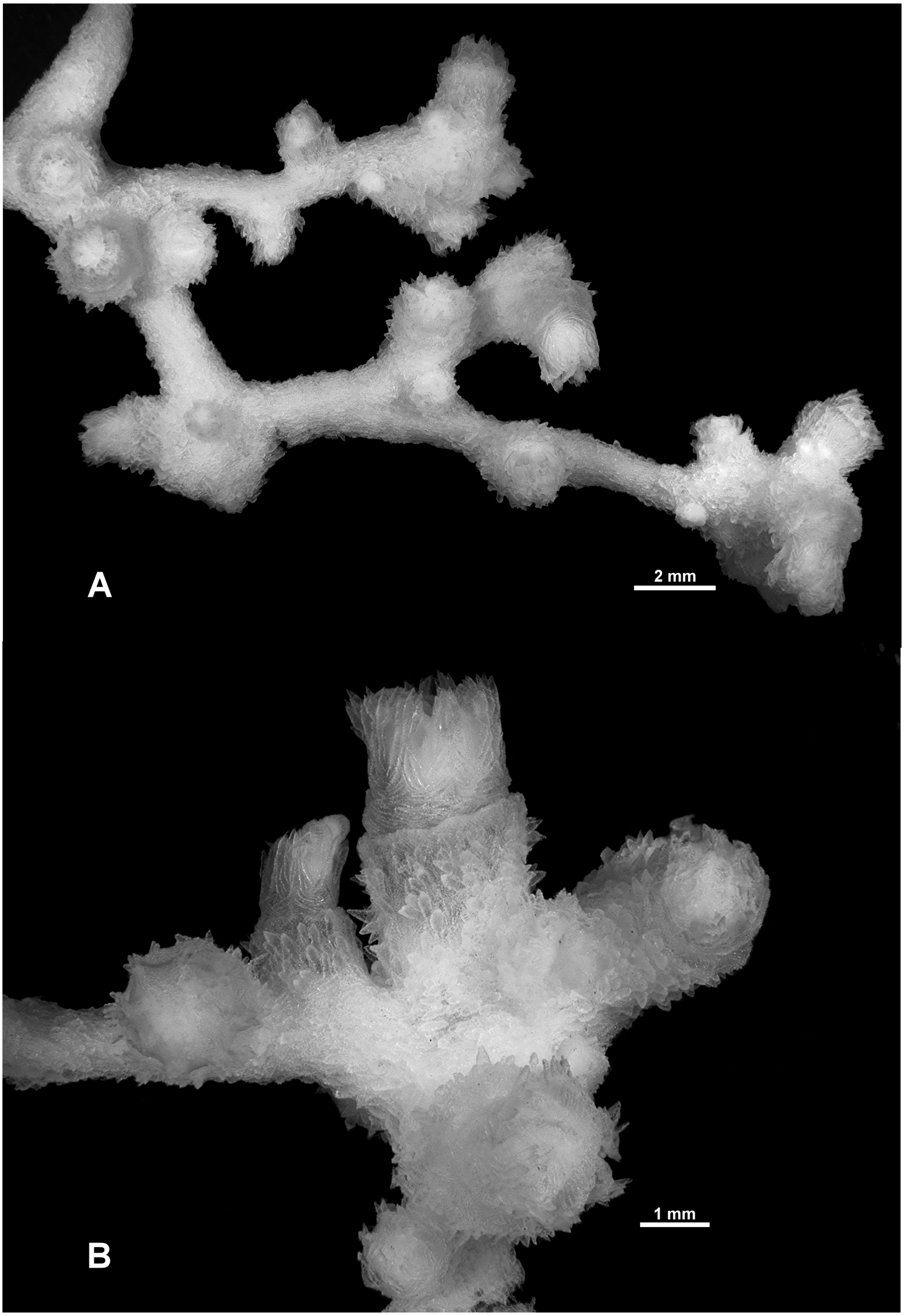

Figure 2.54. *Anthothela quattriniae*, n. sp,, holotype: A. Largest fragment examined; B. Branch tip.

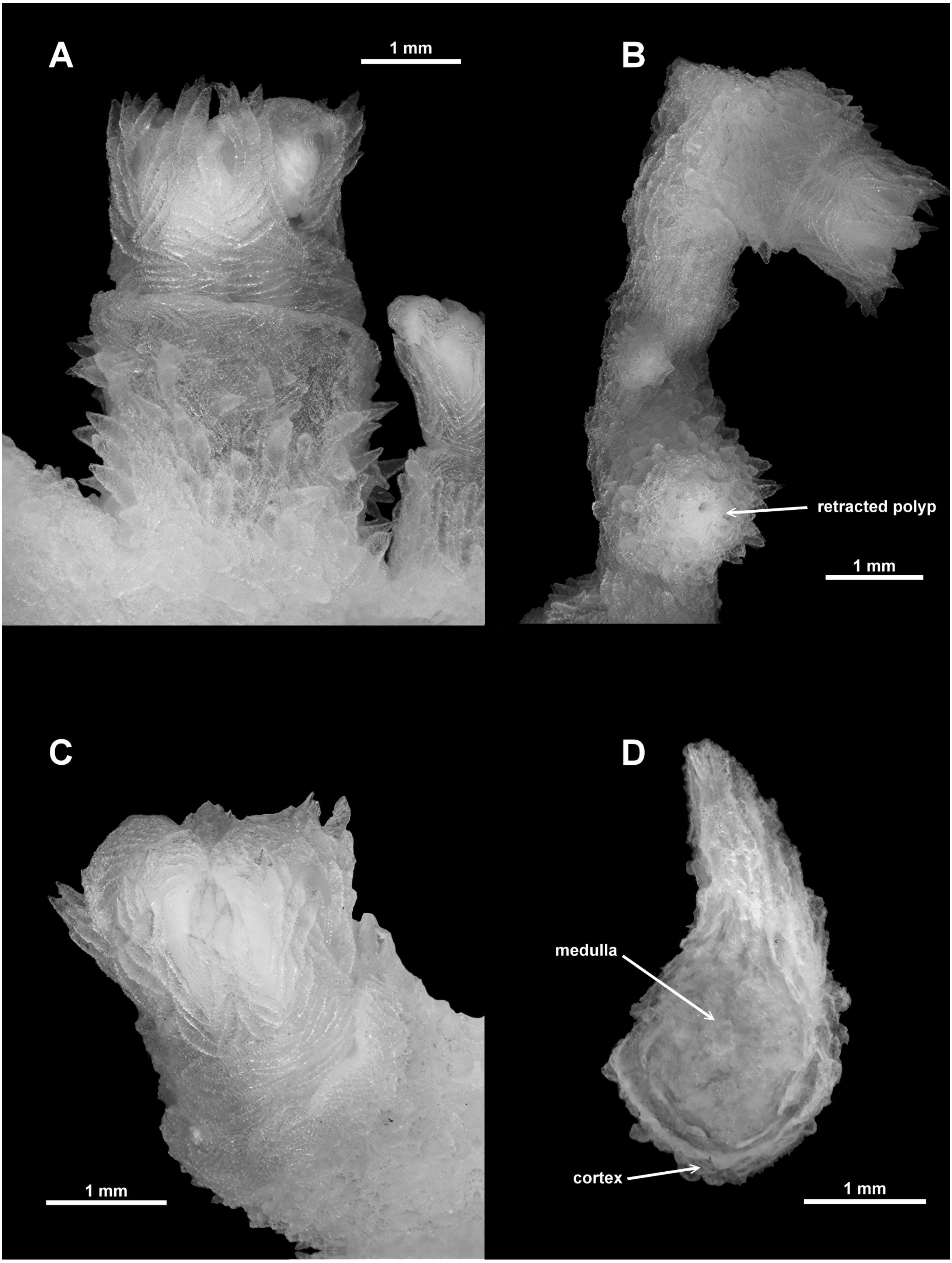

Figure 2.55. *Anthothela quattriniae*, n. sp., holotype: A. Partly retracted polyp; B. Fully retracted polyp; C. Points and back of tentacles; D. Decalcified cross-section of branch.

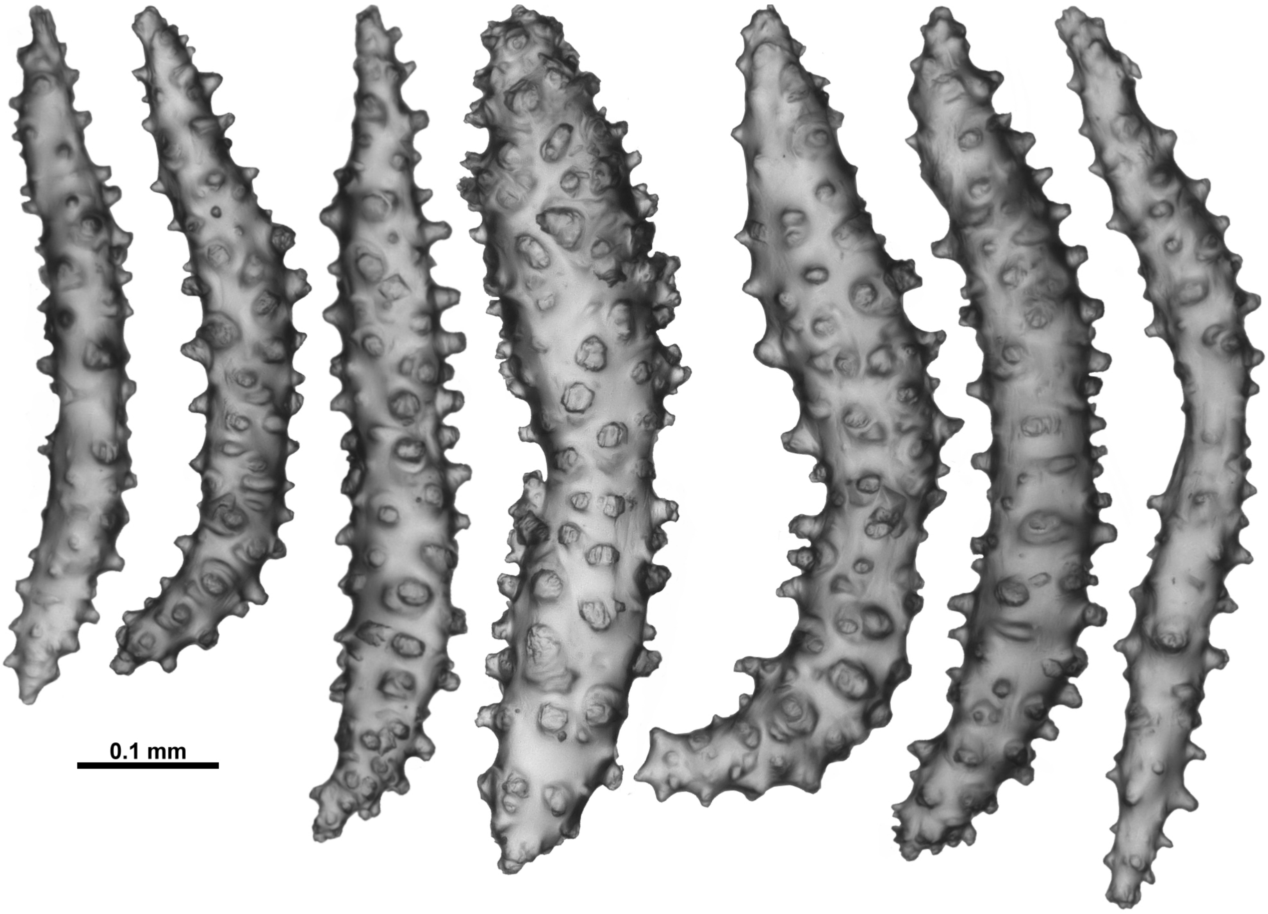

Figure 2.56. *Anthothela quattriniae*, n. sp., holotype: Simple point and collaret sclerites.

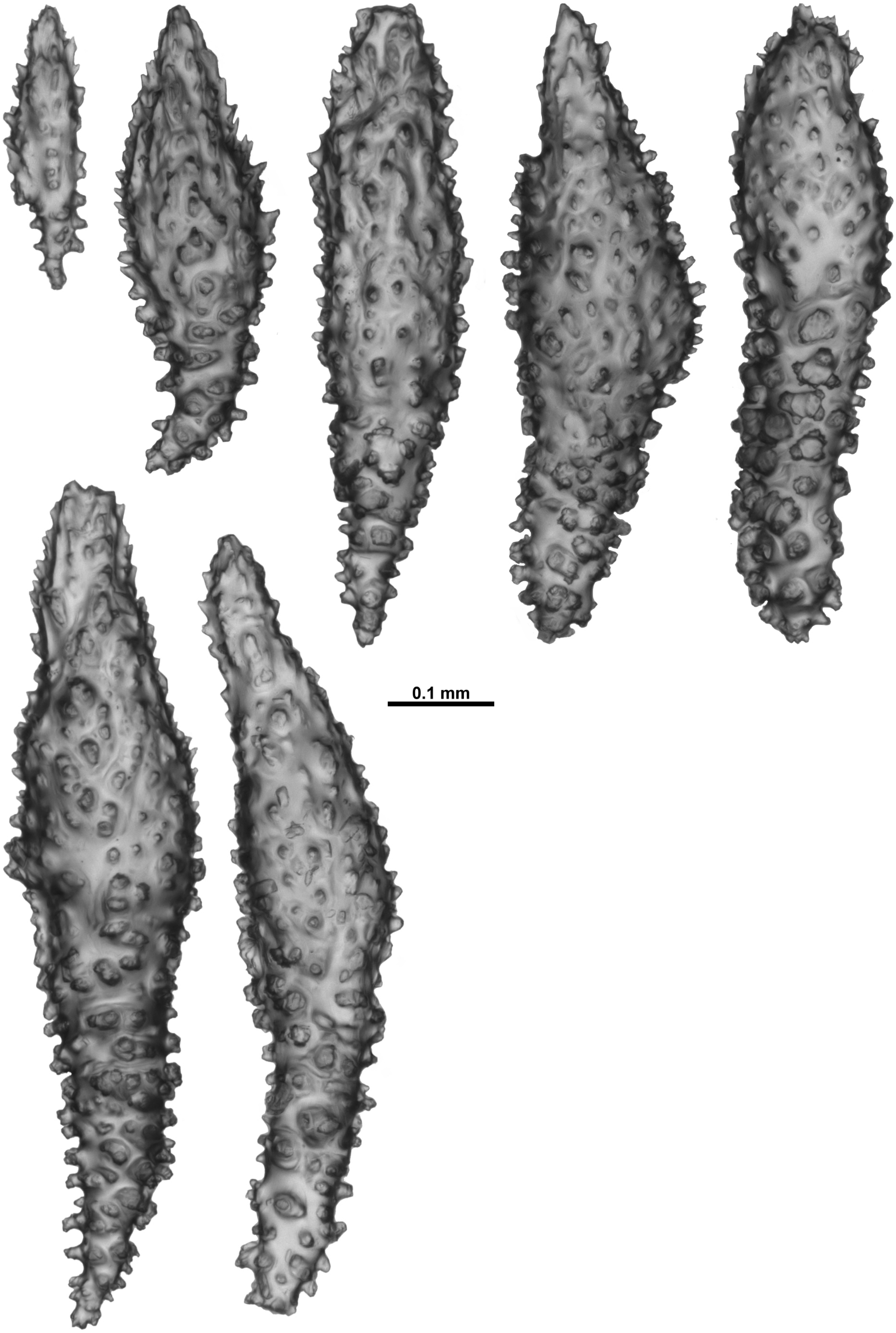

Figure 2.57. *Anthothela quattriniae*, n. sp., holotype: Bulbous point sclerites.

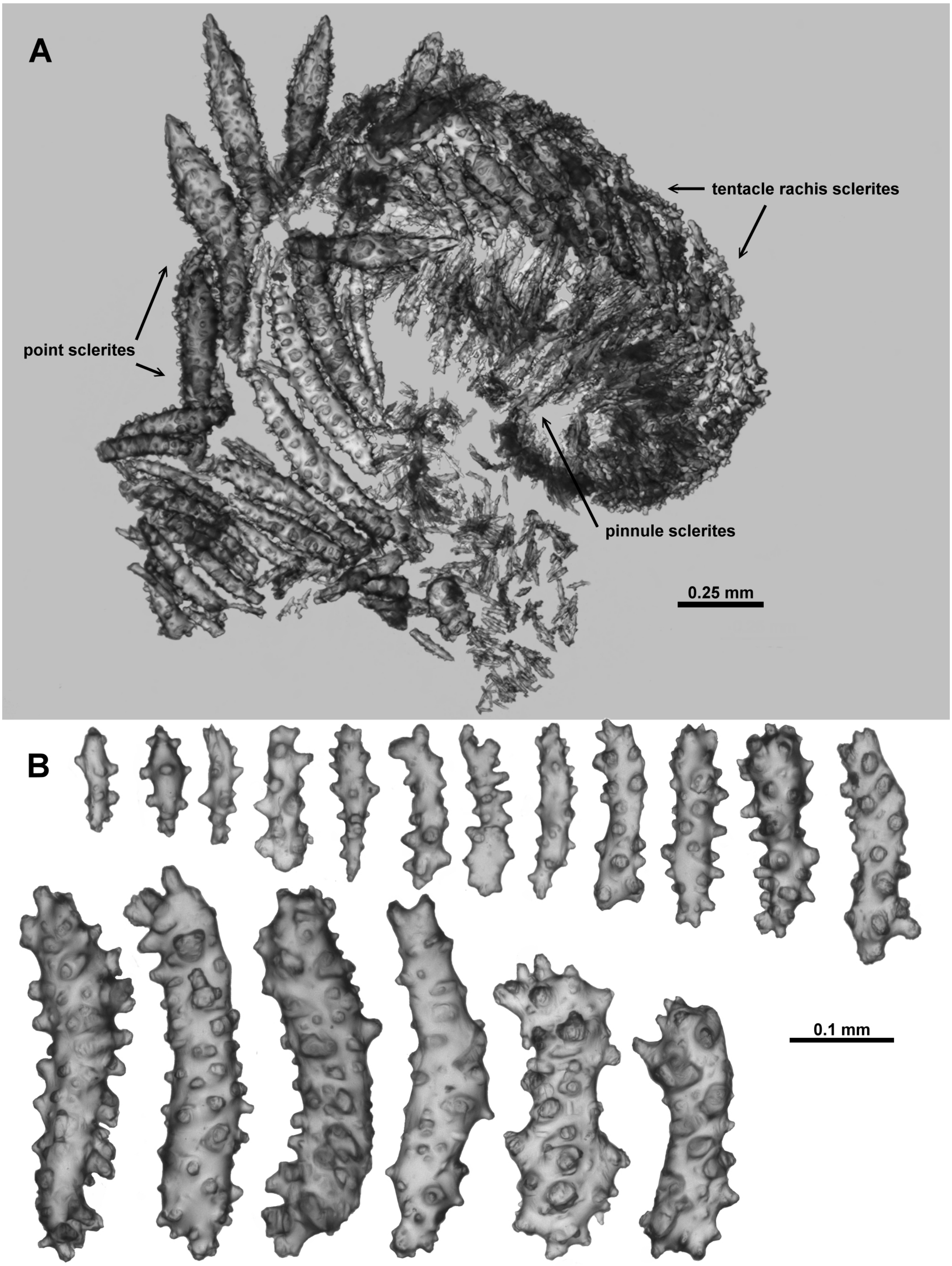

Figure 2.58. *Anthothela quattriniae*, n. sp., holotype: A. Tentacle and point sclerites in situ; B. Tentacle rachis sclerites.

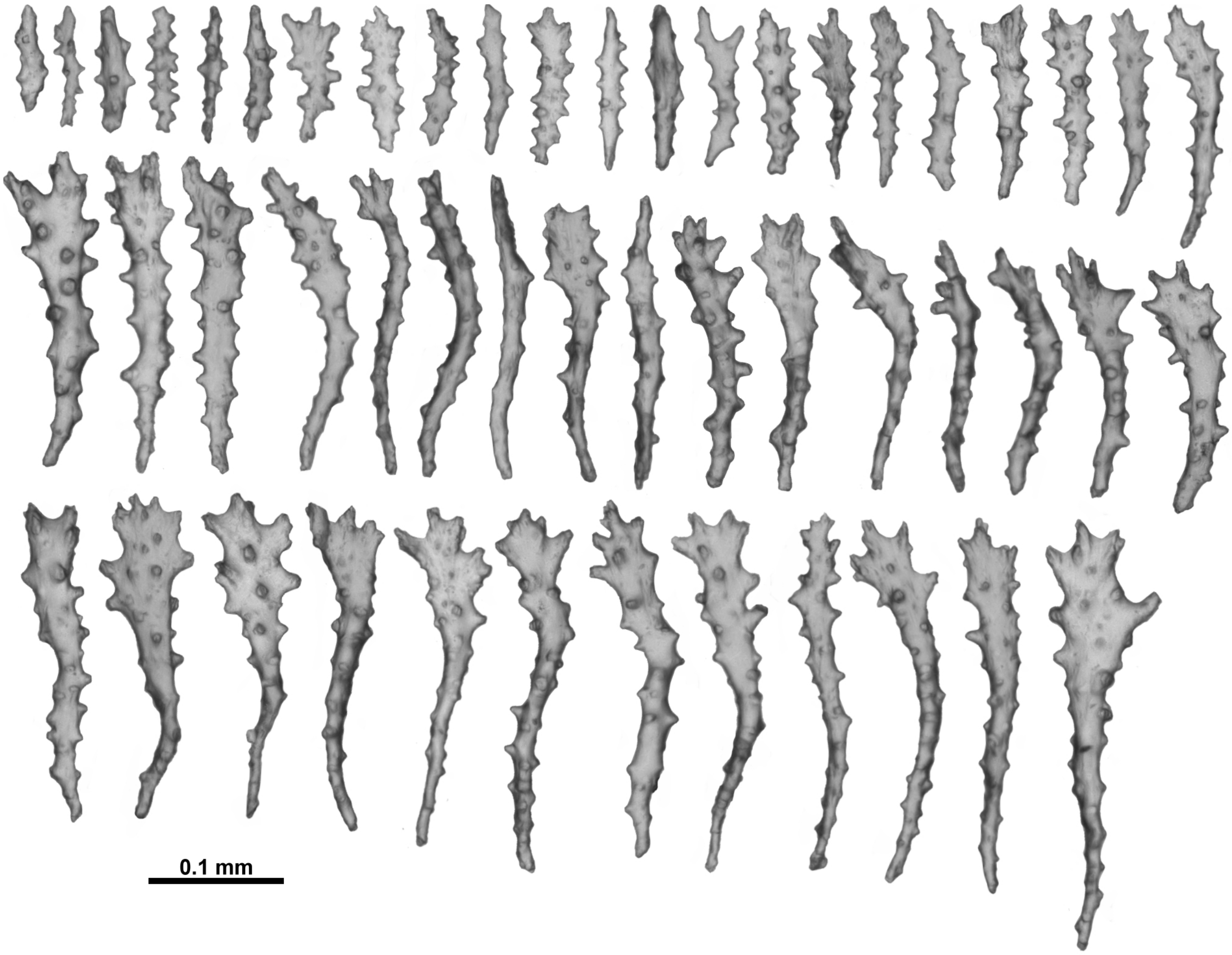

Figure 2.59. *Anthothela quattriniae*, n. sp., holotype, sclerites: Pinnule.

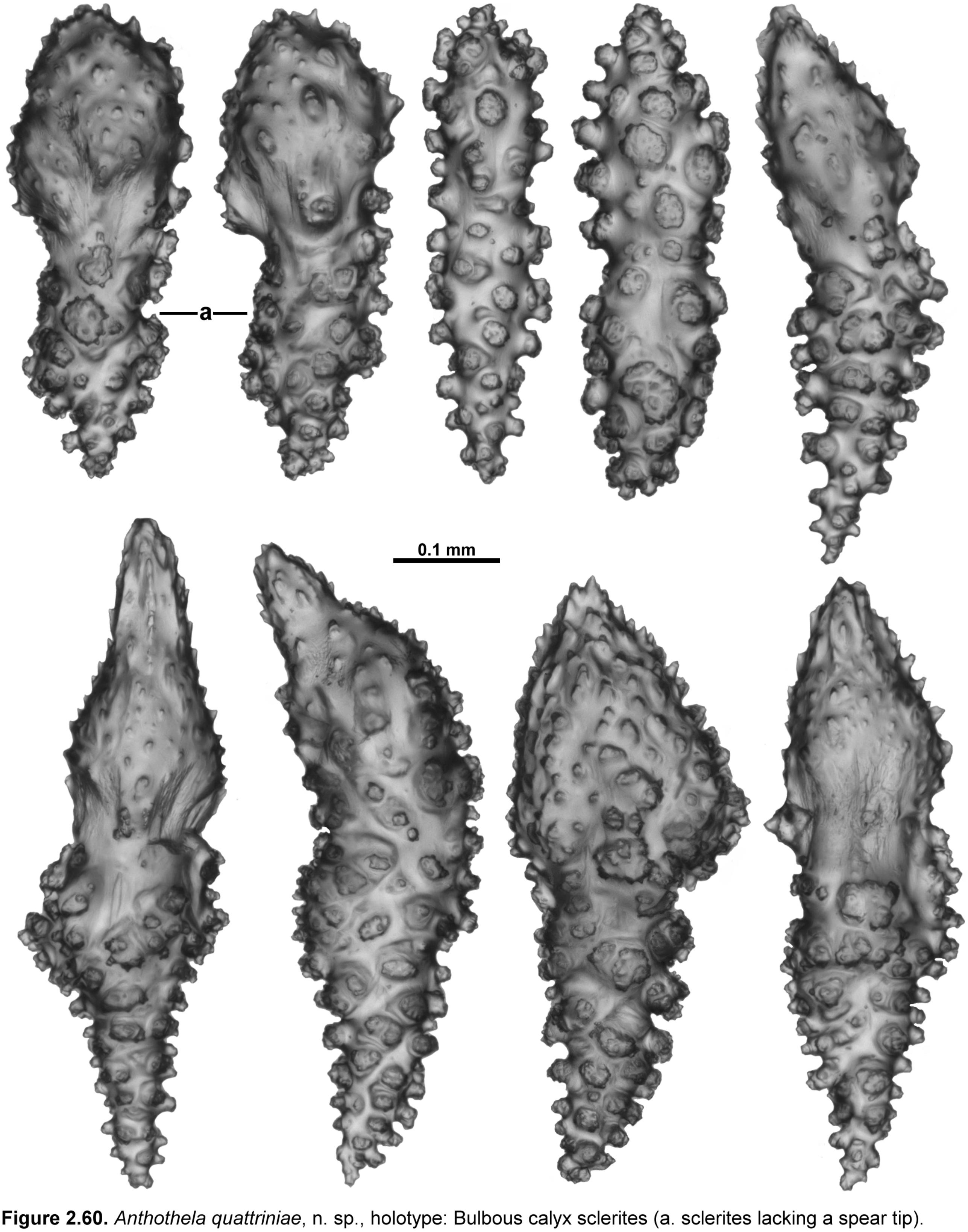

Figure 2.60. *Anthothela quattriniae*, n. sp., holotype: Bulbous calyx sclerites (a. sclerites lacking a spear tip).

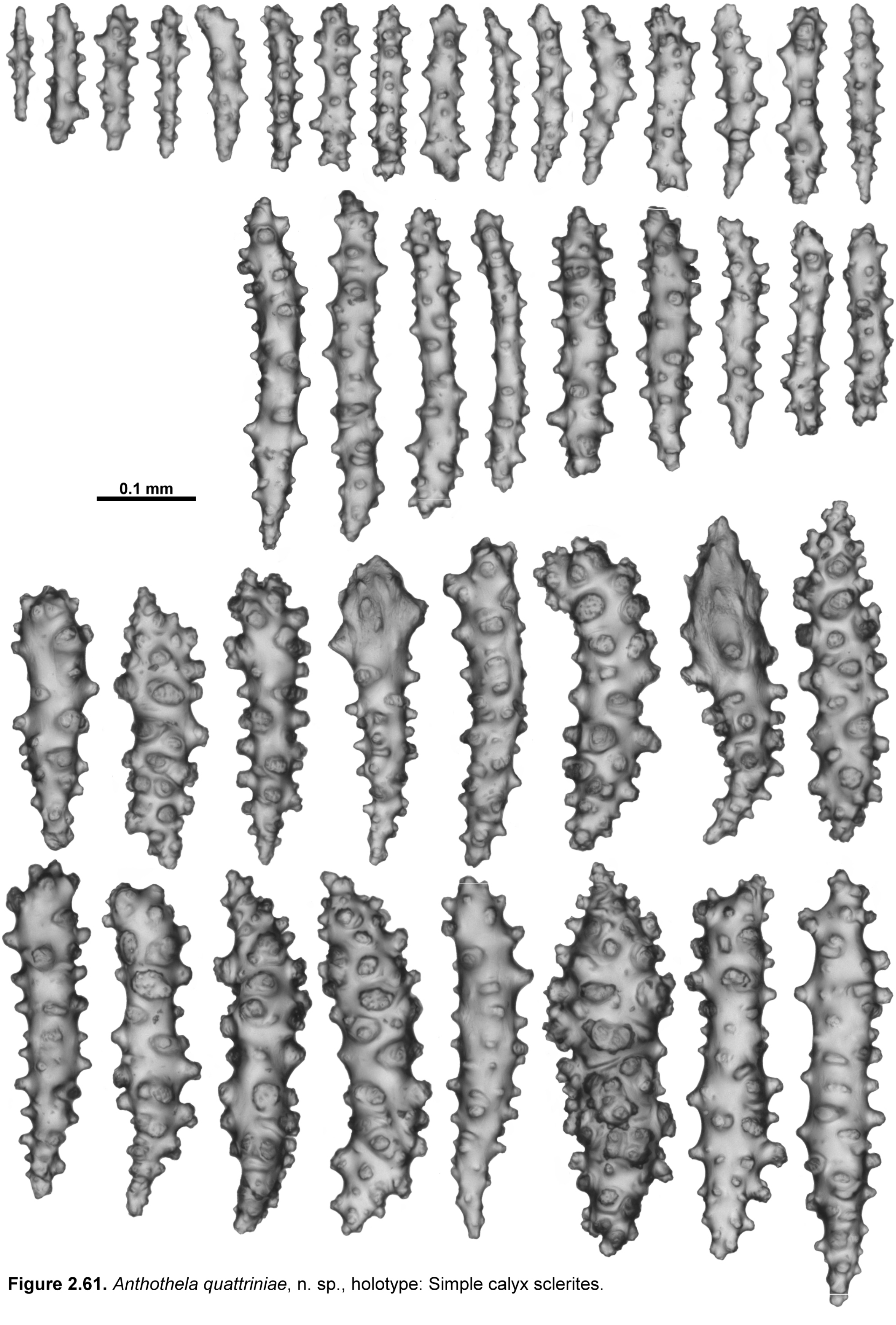

Figure 2.61. *Anthothela quattriniae*, n. sp., holotype: Simple calyx sclerites.

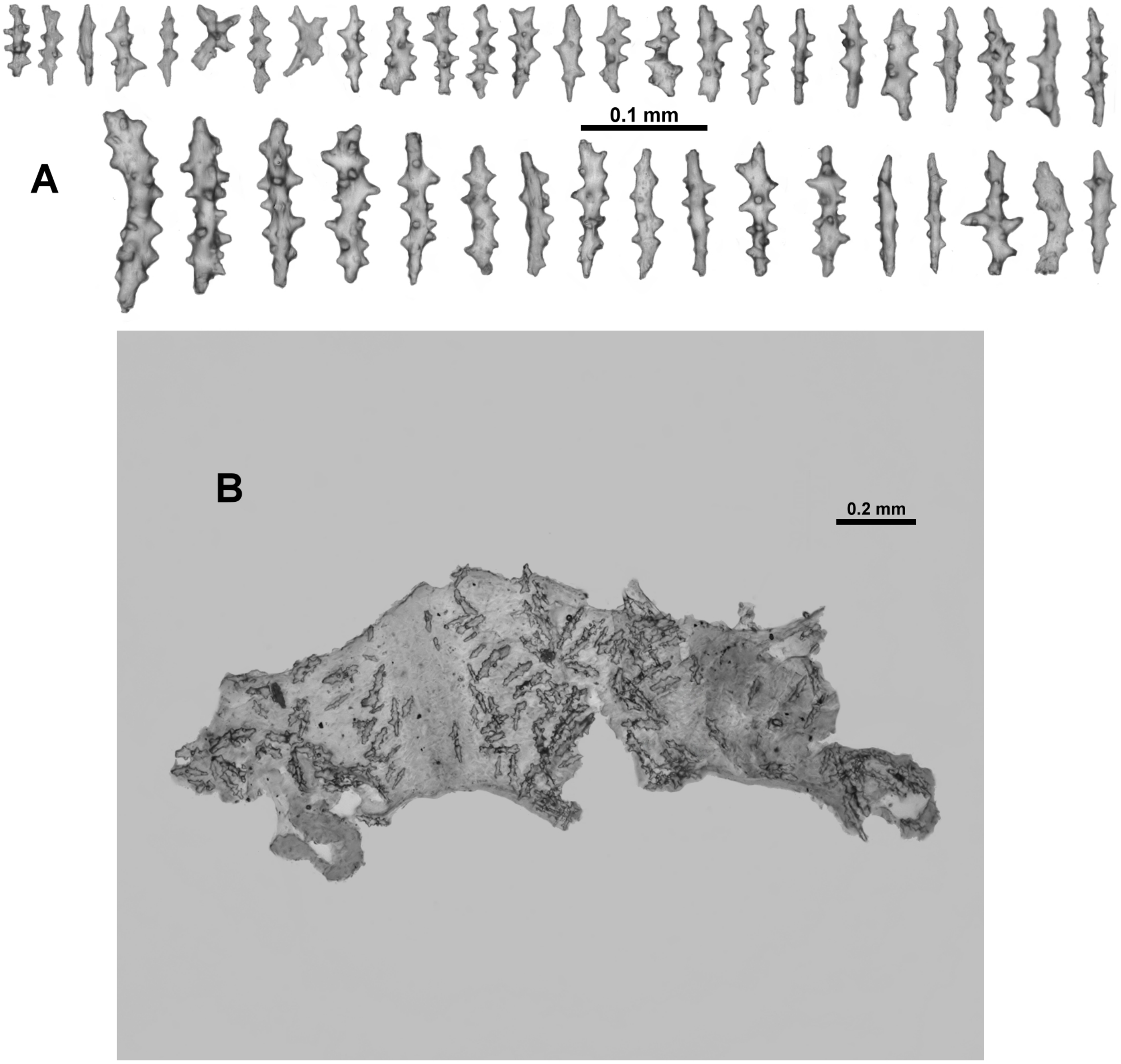

Figure 2.62. *Anthothela quattriniae*, n. sp., holotype: A. Pharynx sclerites; B. In situ arrangement of pharynx sclerites.

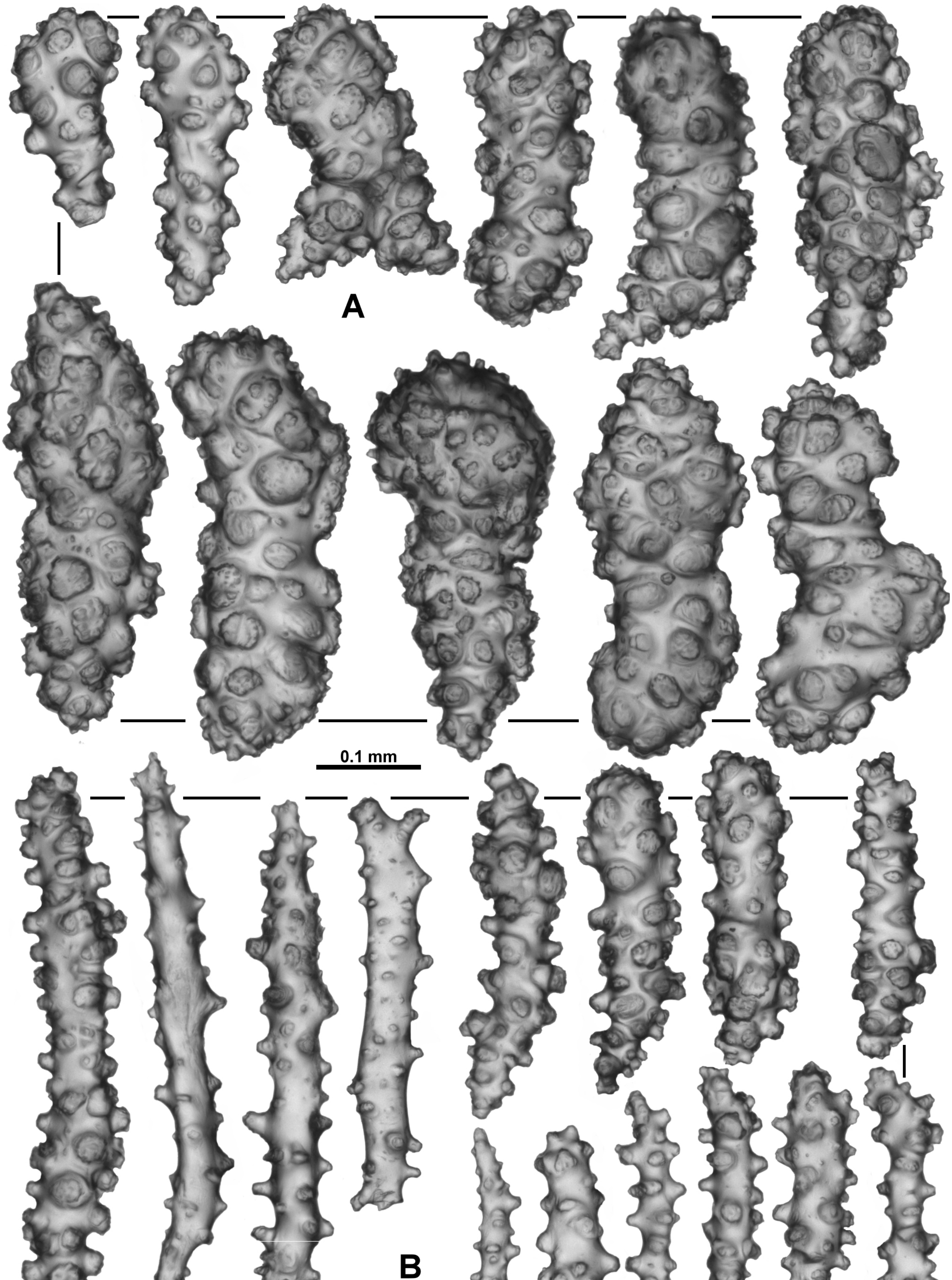

Figure 2.63. *Anthothela quattriniae*, n. sp., holotype: A. Bulbous cortex sclerites; B. Simple cortex sclerites.

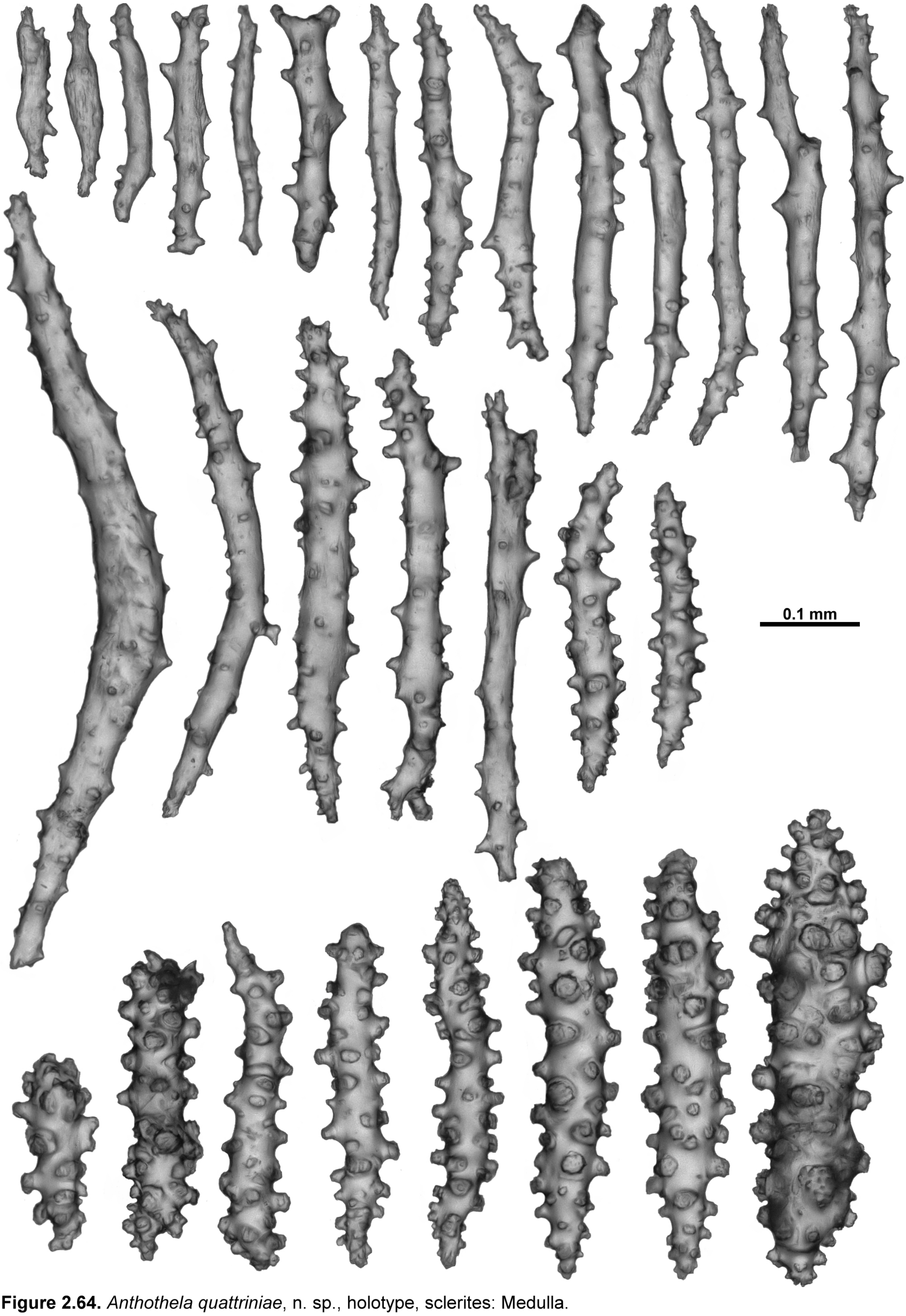

Figure 2.64. *Anthothela quattriniae*, n. sp., holotype, sclerites: Medulla.

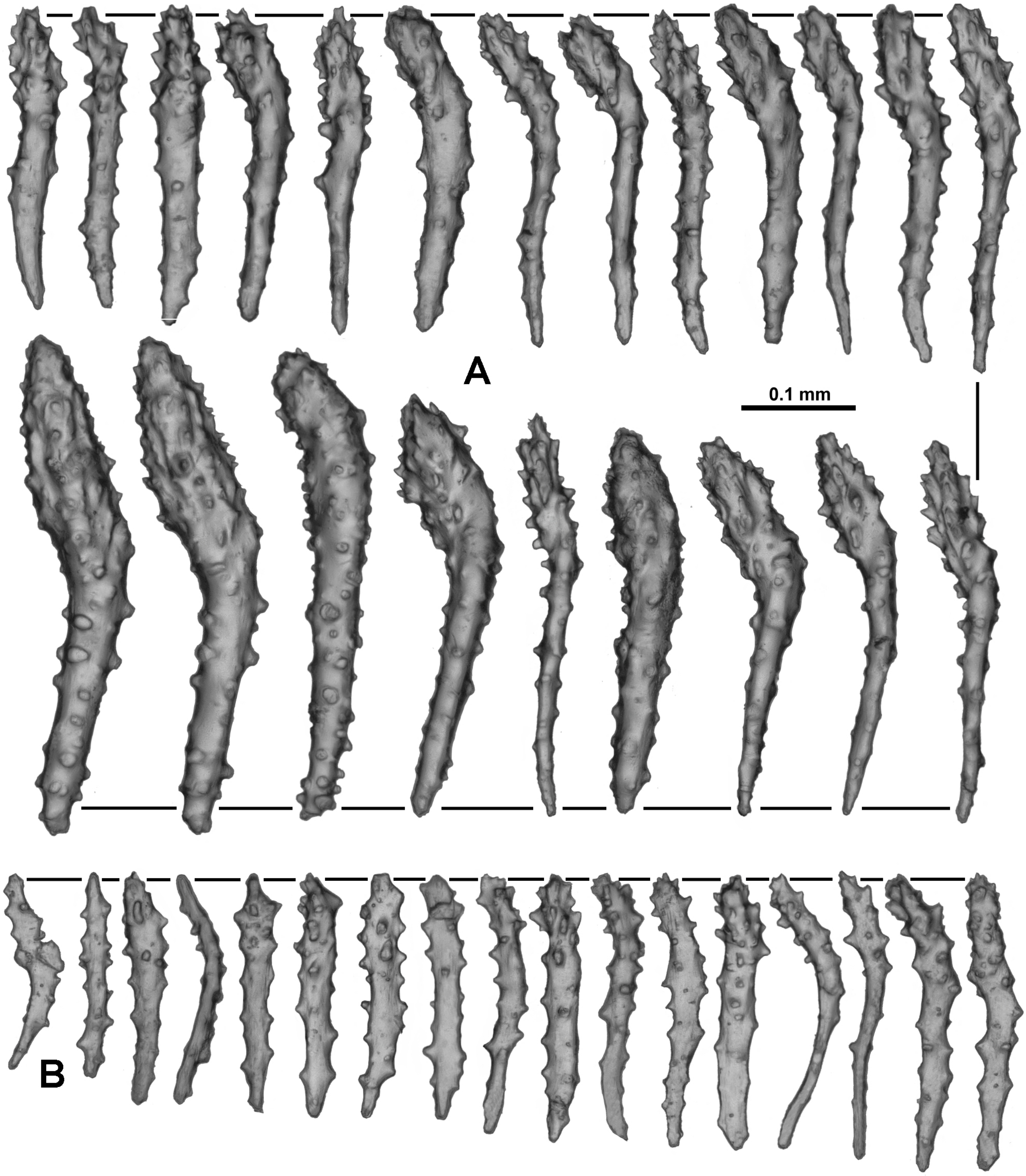

Figure 2.65. *Victorgorgia josephinae* López-González and Briand, 2002*,* holotype, sclerites: A. Tentacle rachis; B. Pinnule.

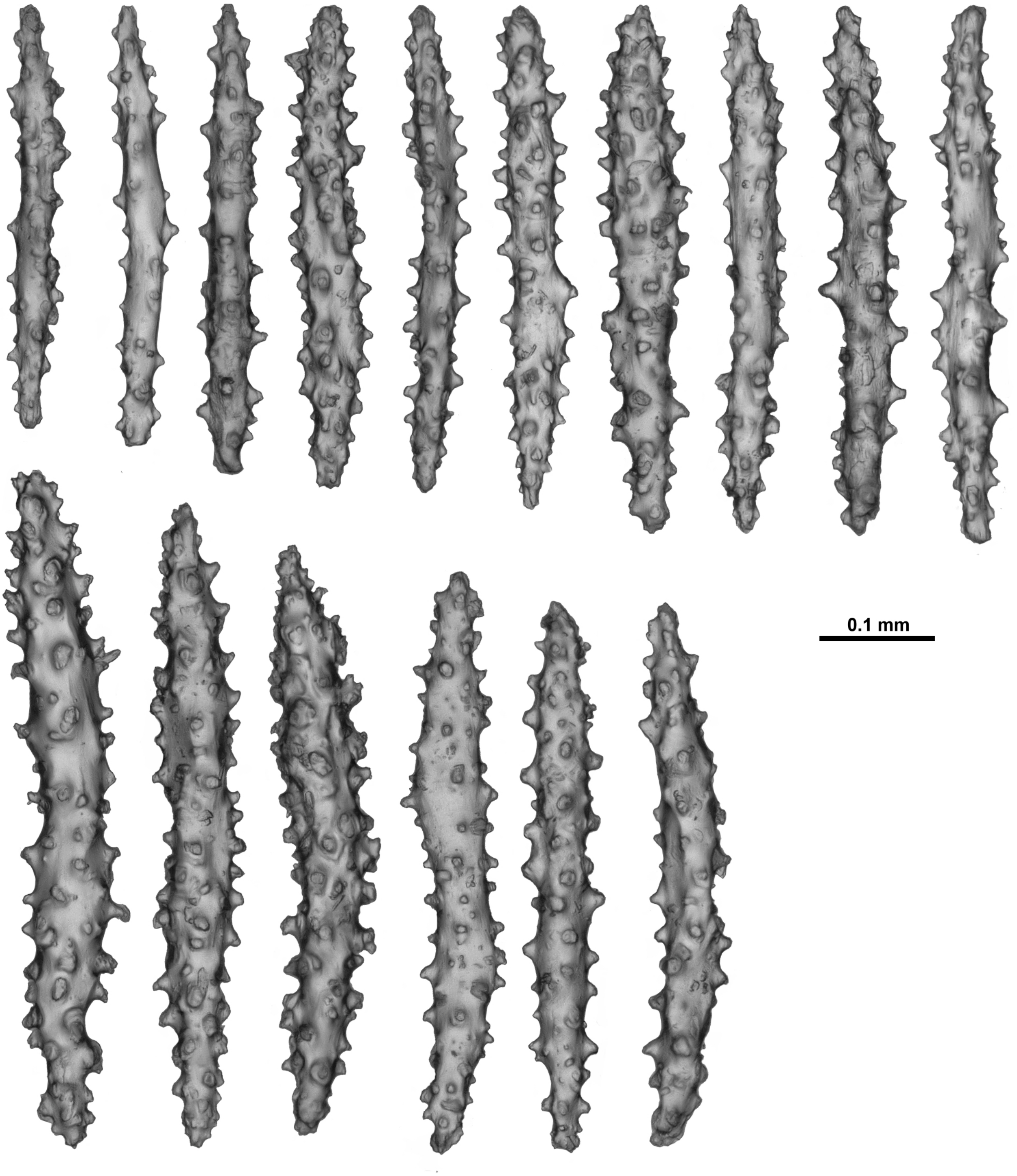

Figure 2.66. *Victorgorgia josephinae,* López-González and Briand, 2002, holotype, sclerites: Calyx.

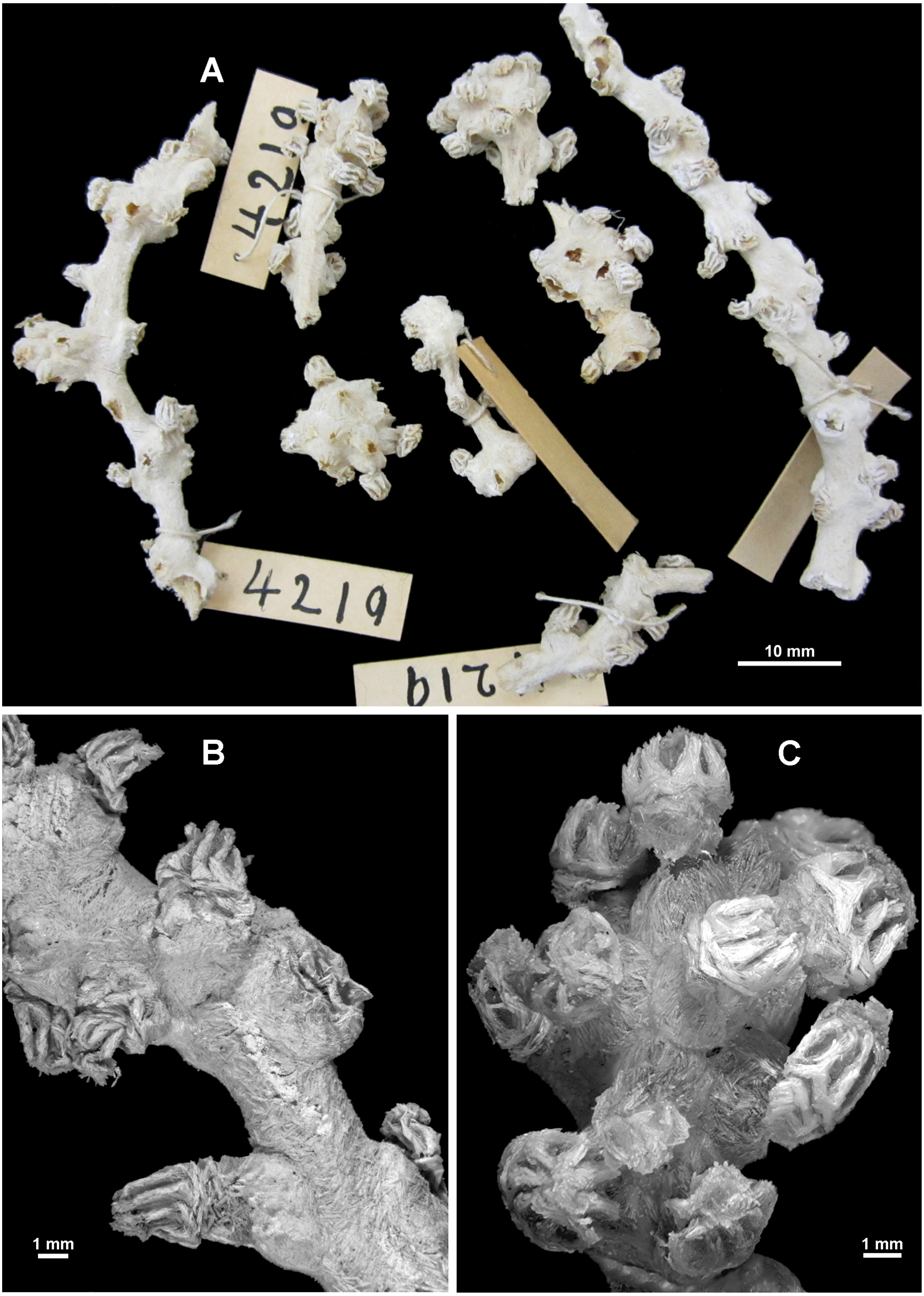

Figure 2.67. *Victorgorgia argentea* (Studer, 1894), holotype: A. Colony; B. Dried branch with polyps; C. Rehydrated polyp bunch at branch tip.

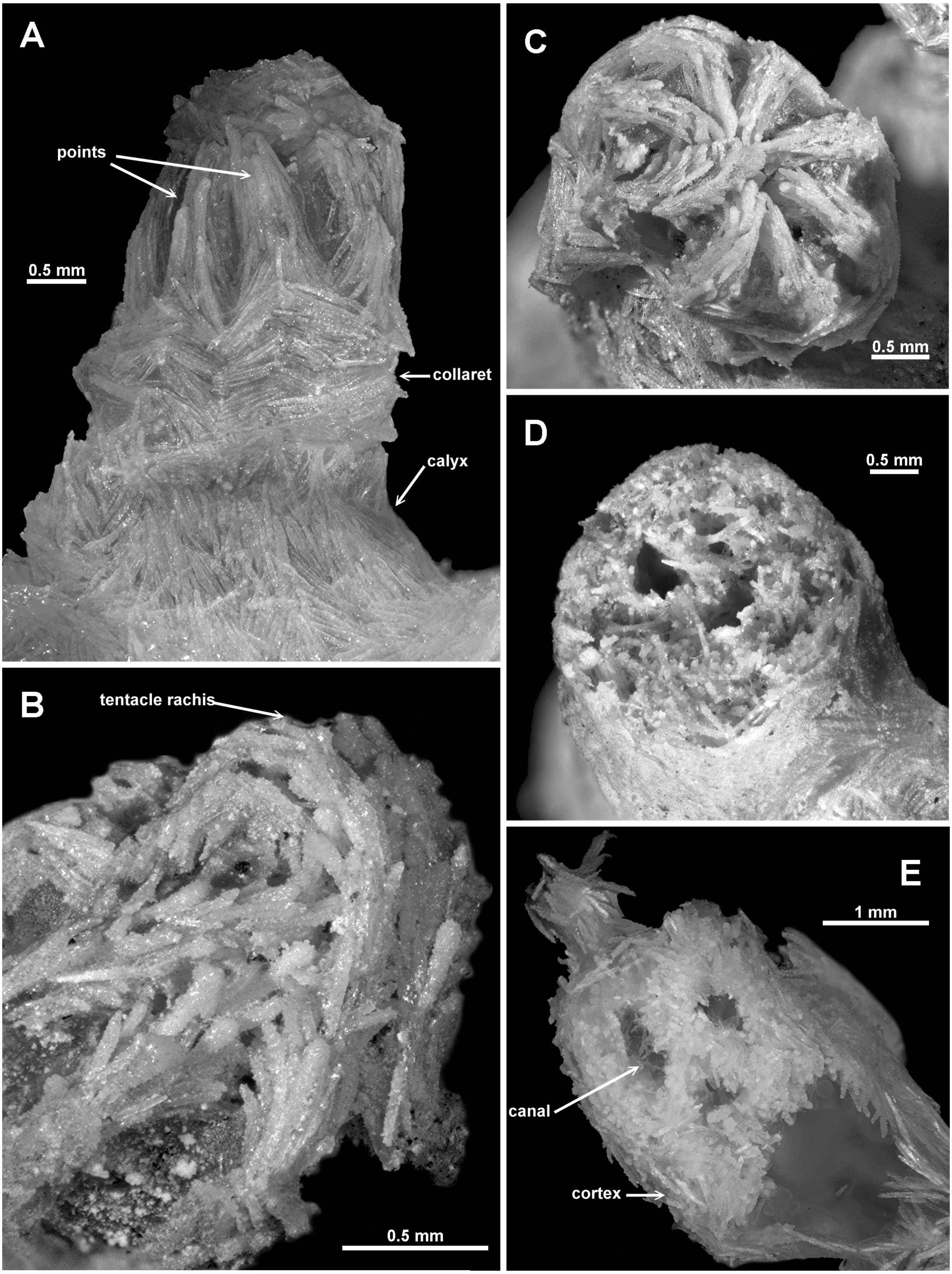

Figure 2.68. *Victorgorgia argentea* (Studer, 1894), holotype: A. Polyp; B. Tentacles bunched over polyp mouth; C. Tentacles folded over polyp mouth; D. Cross-section of dried branch; E. Cross-section of rehydrated branch.

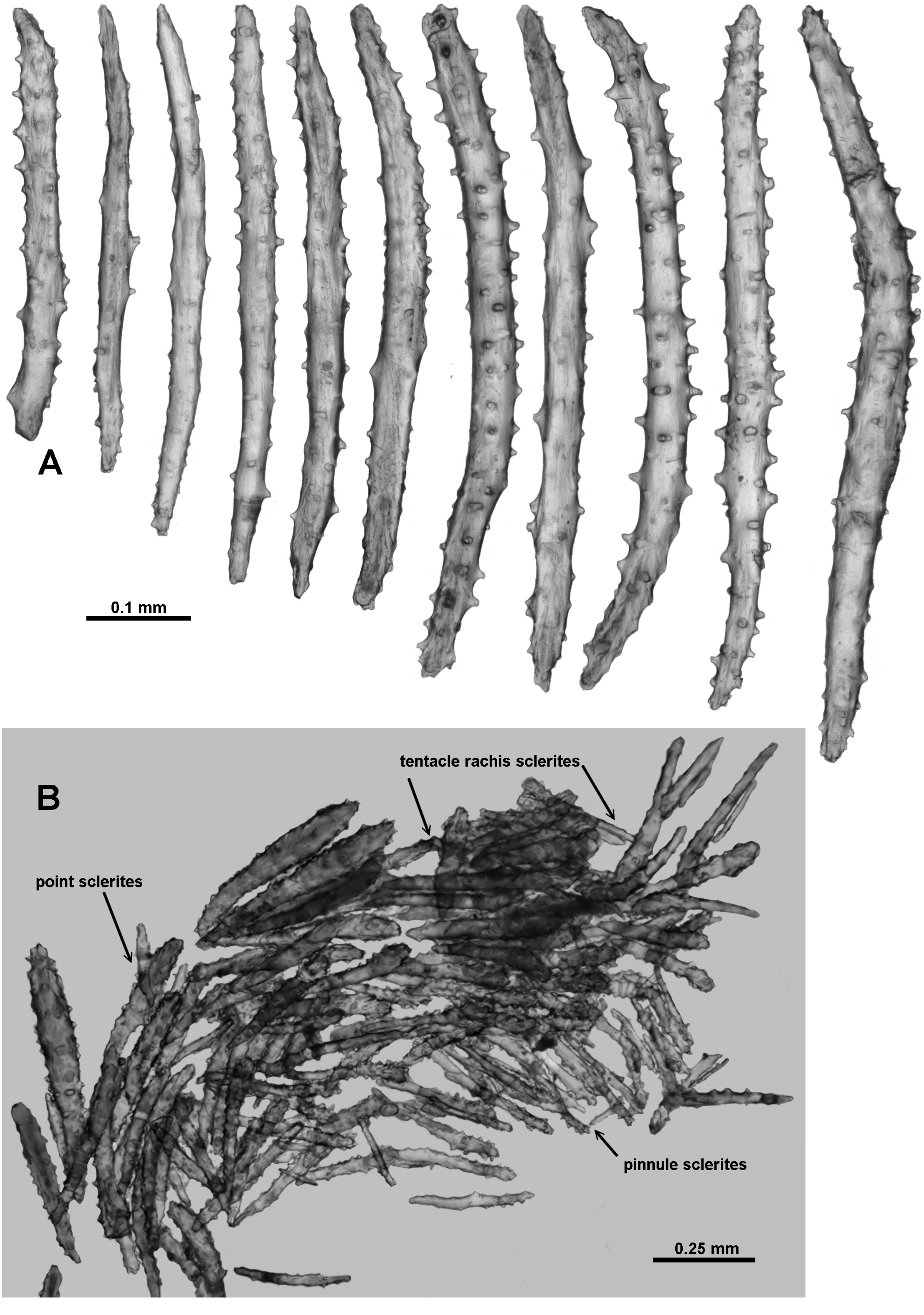

Figure 2.69. *Victorgorgia argentea* (Studer, 1894), holotype: A. Slender point sclerites; B. Tentacle and point sclerites in situ.

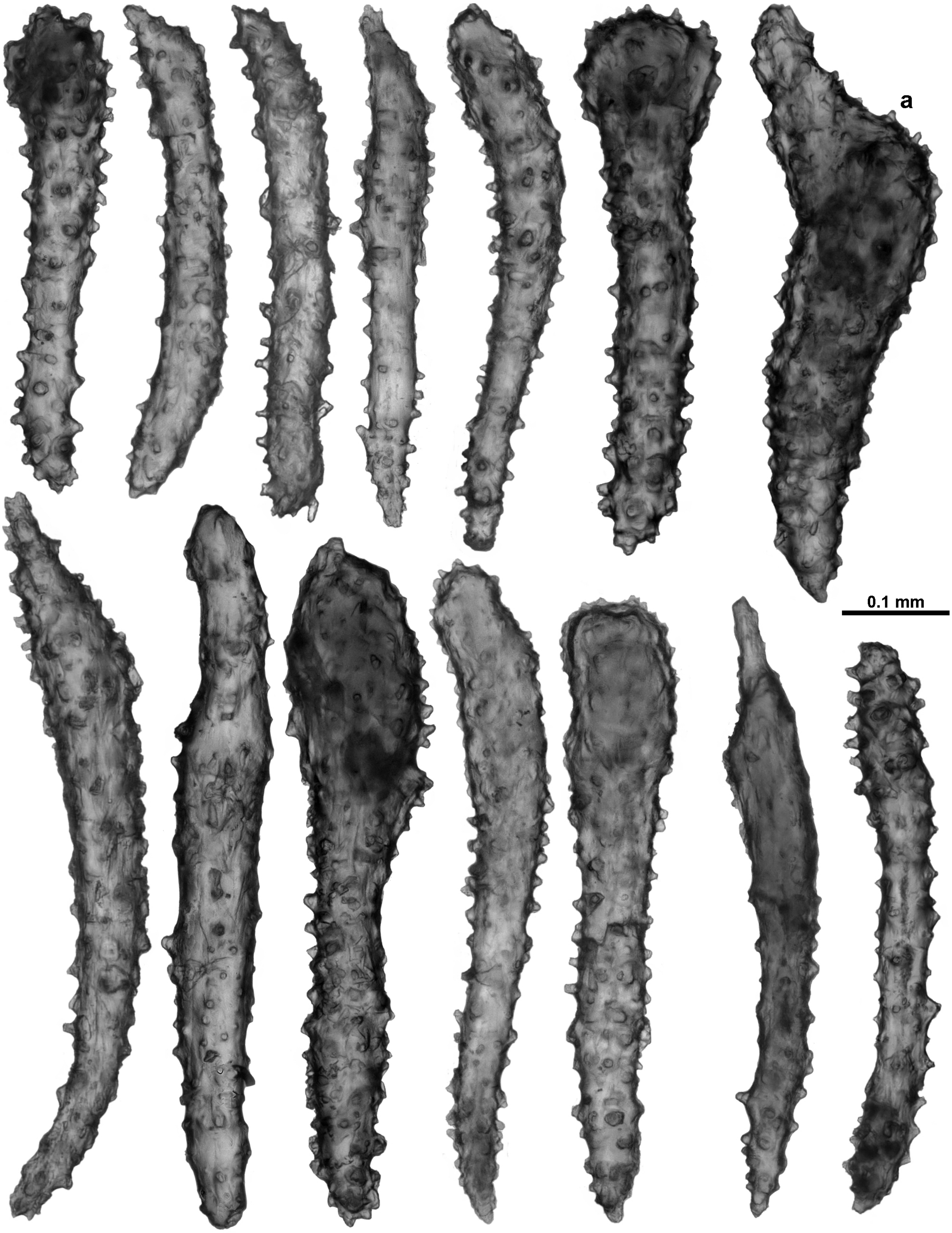

Figure 2.70. *Victorgorgia argentea* (Studer, 1894), holotype: Large point sclerites (a. bent spindle).

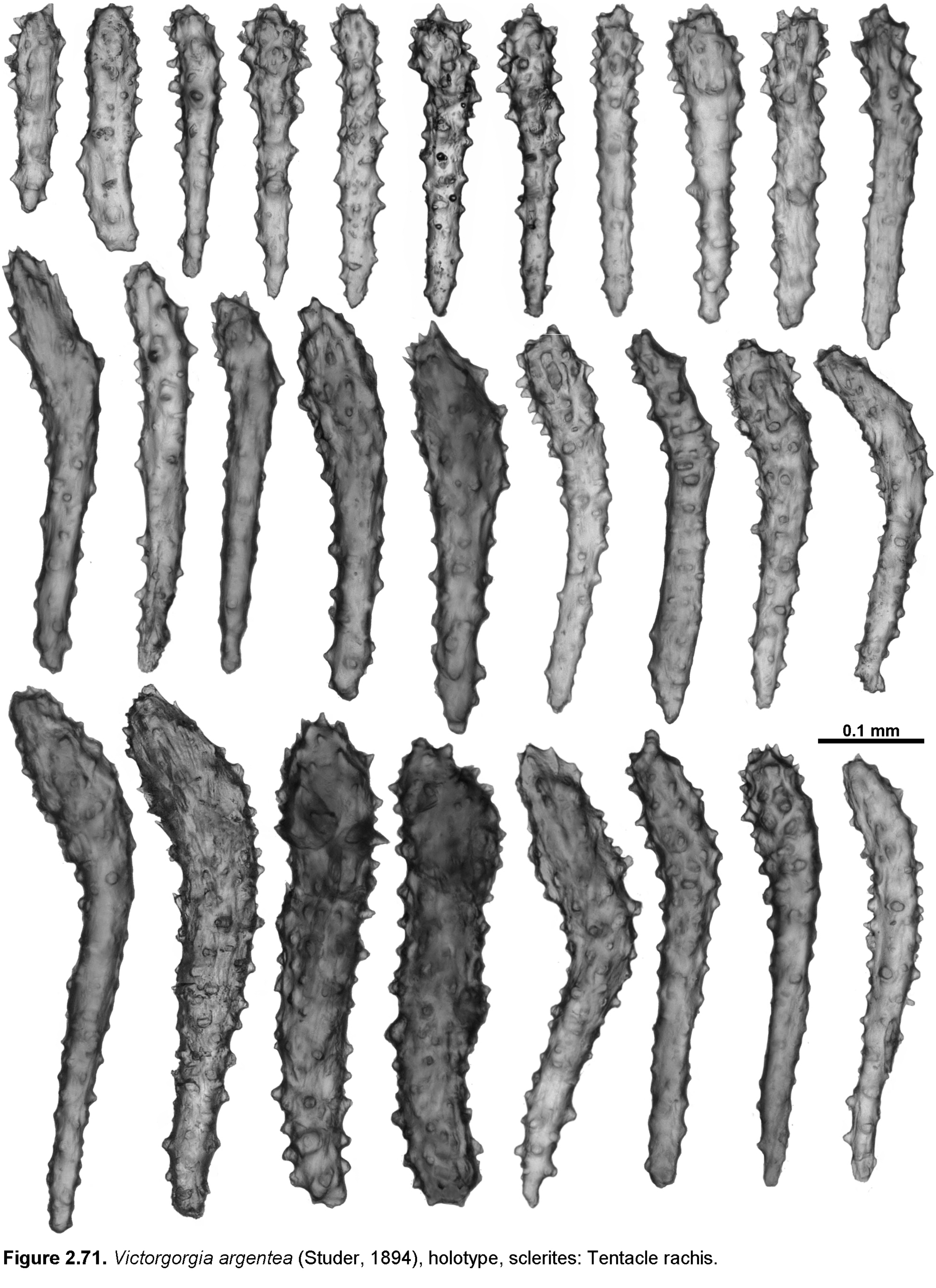

Figure 2.71. *Victorgorgia argentea* (Studer, 1894), holotype, sclerites: Tentacle rachis.

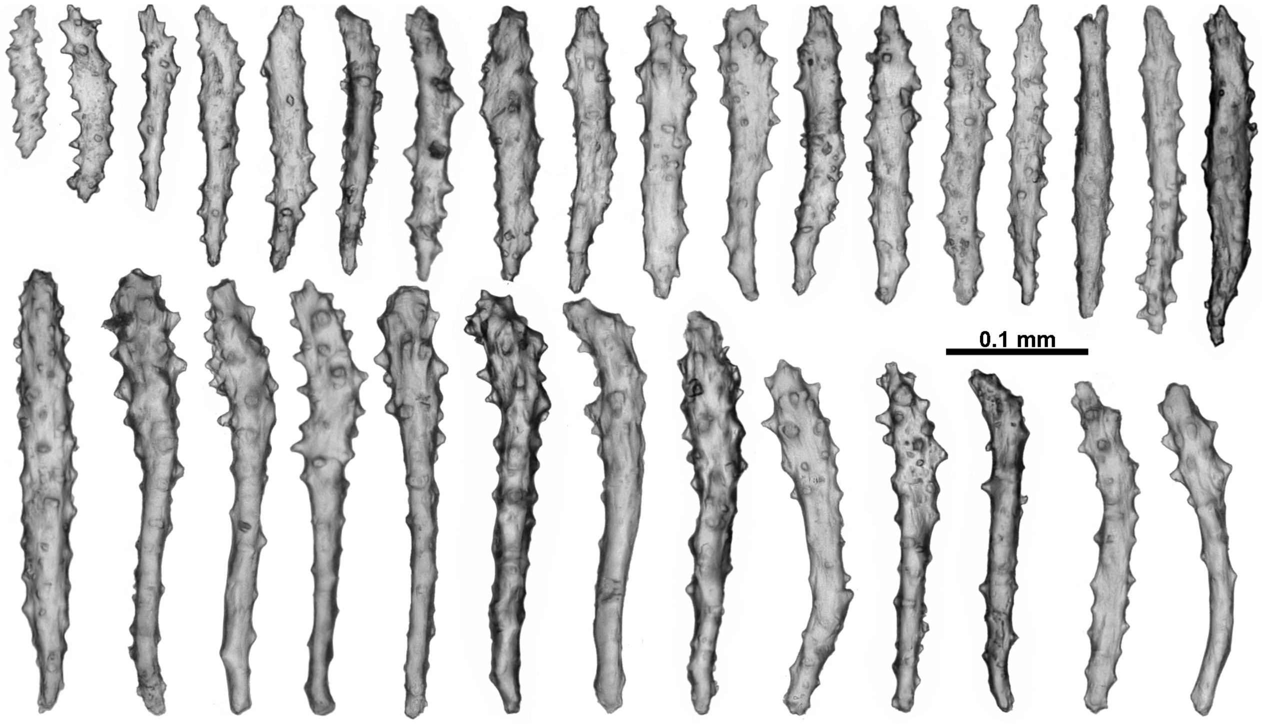

Figure 2.72. *Victorgorgia argentea* (Studer, 1894), holotype, sclerites: Pinnule.

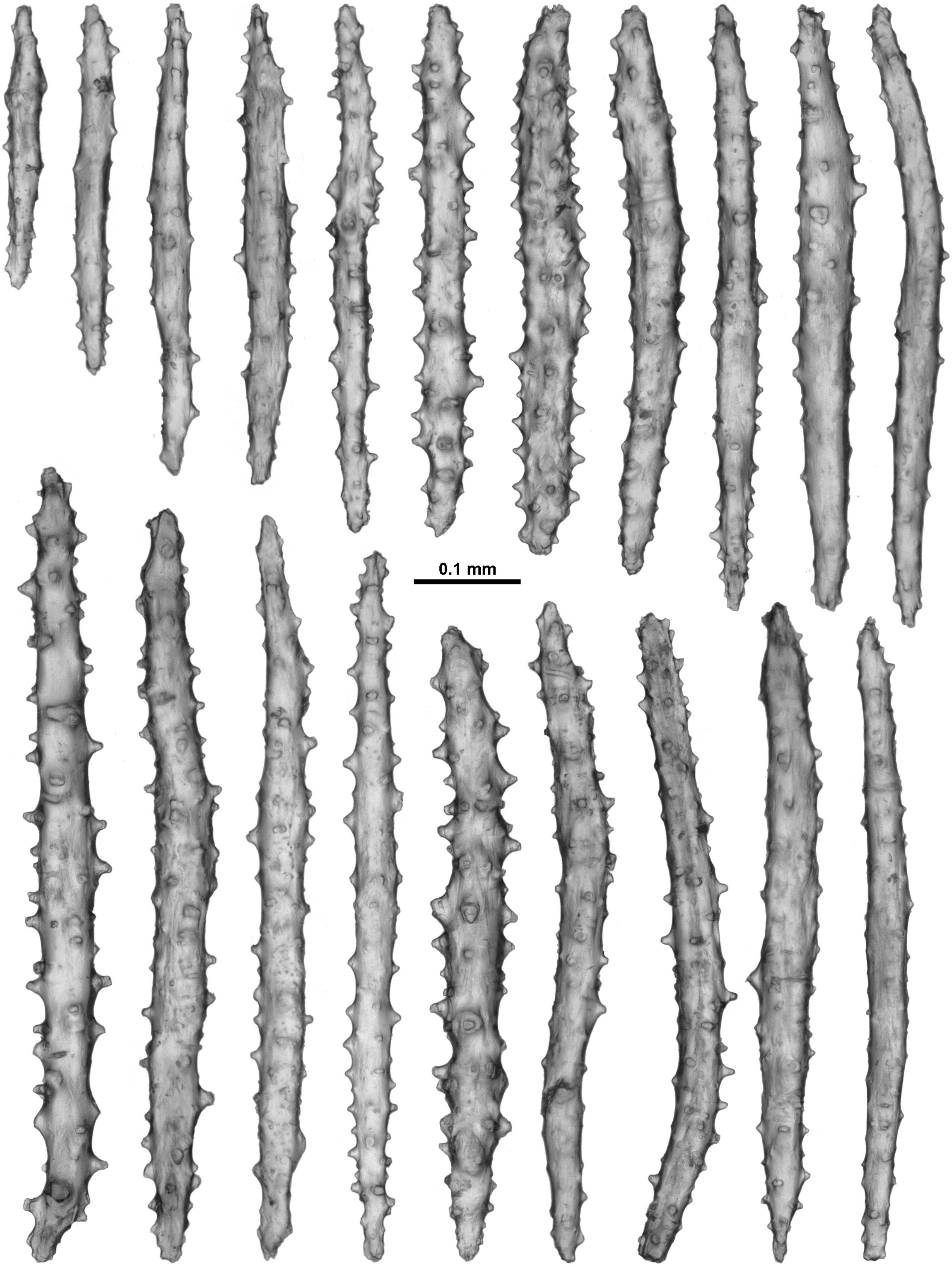

Figure 2.73. *Victorgorgia argentea* (Studer, 1894), holotype, sclerites: Calyx.

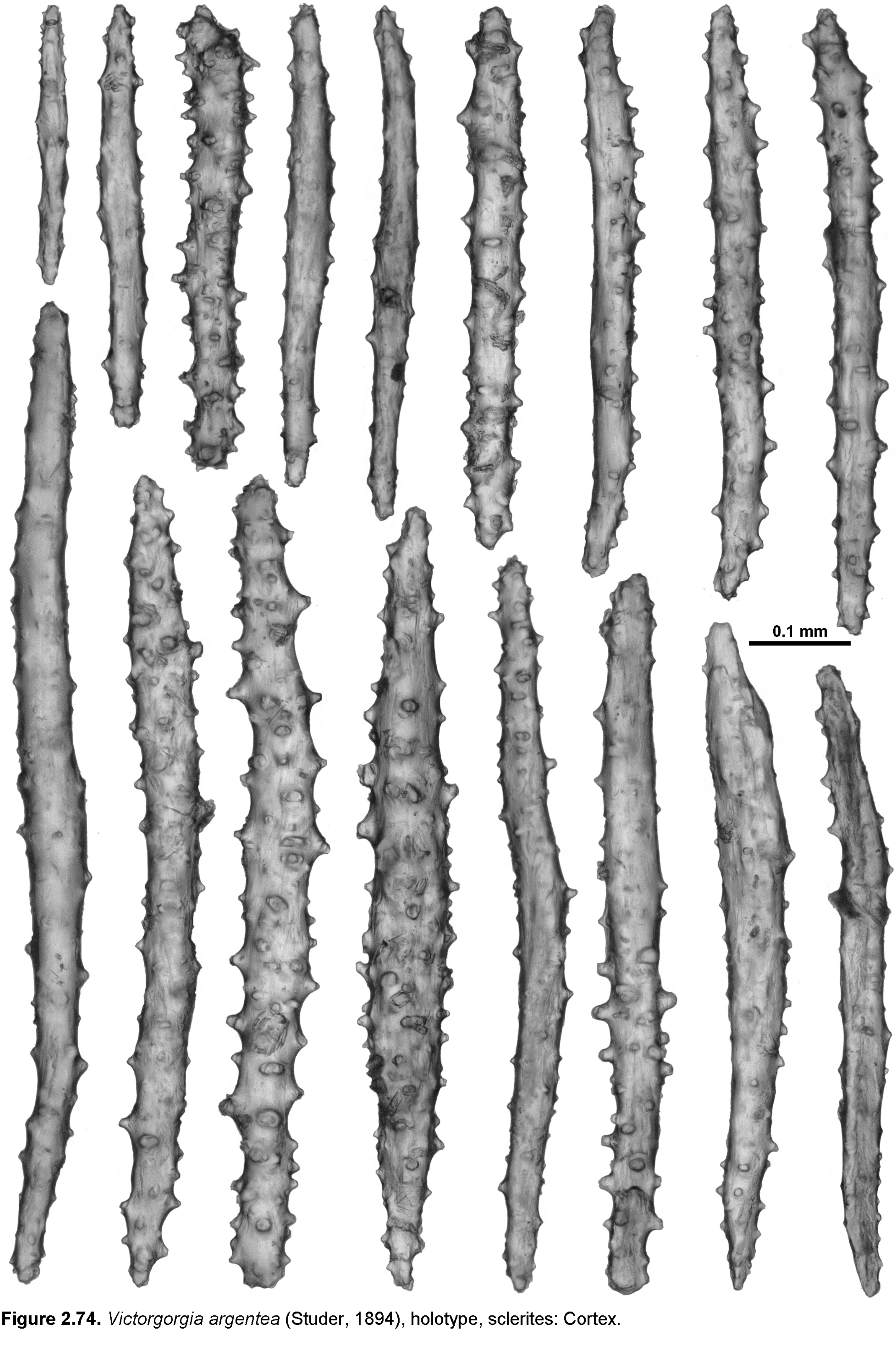

Figure 2.74. *Victorgorgia argentea* (Studer, 1894), holotype, sclerites: Cortex.

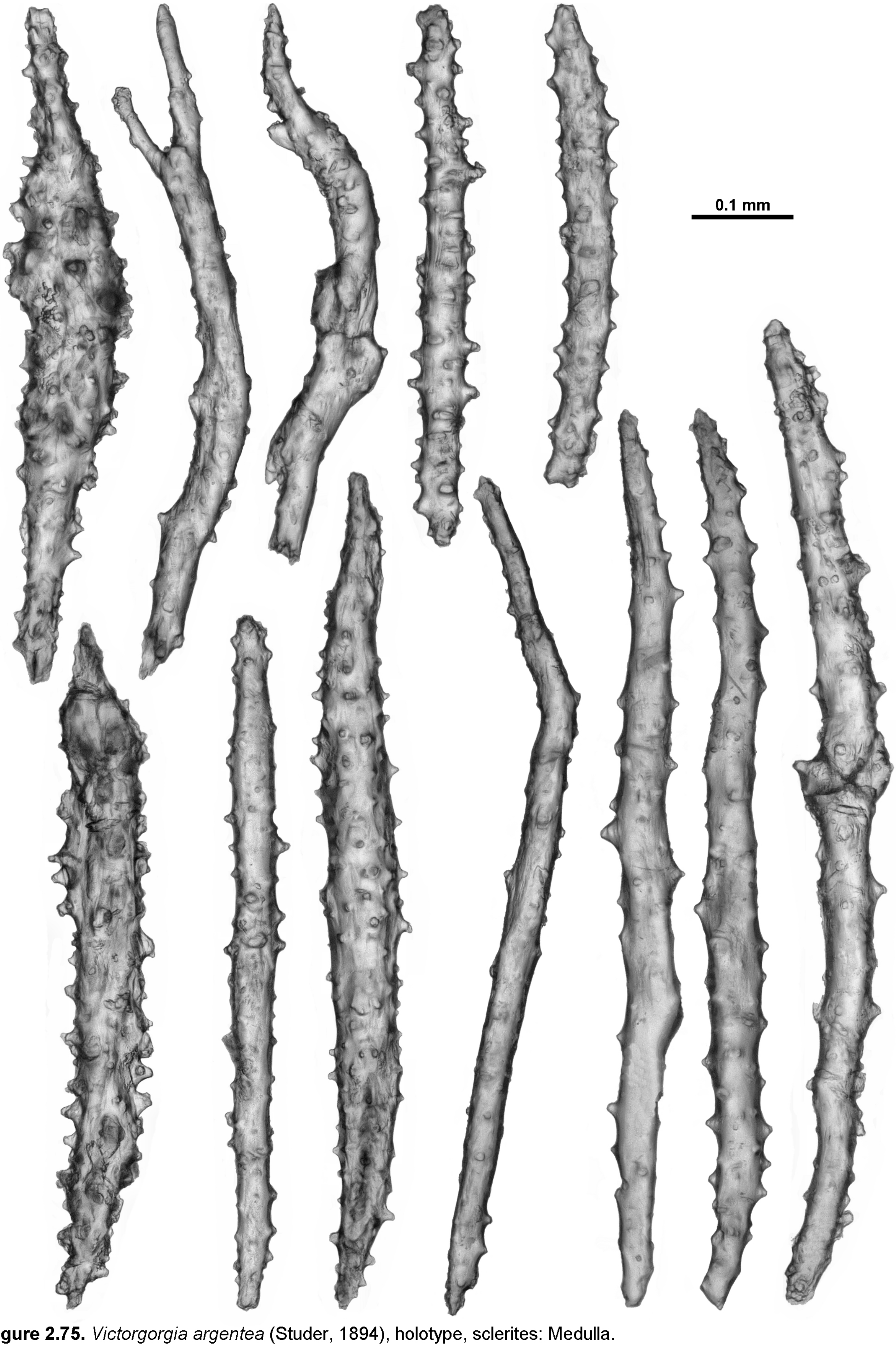

Figure 2.75. *Victorgorgia argentea* (Studer, 1894), holotype, sclerites: Medulla.

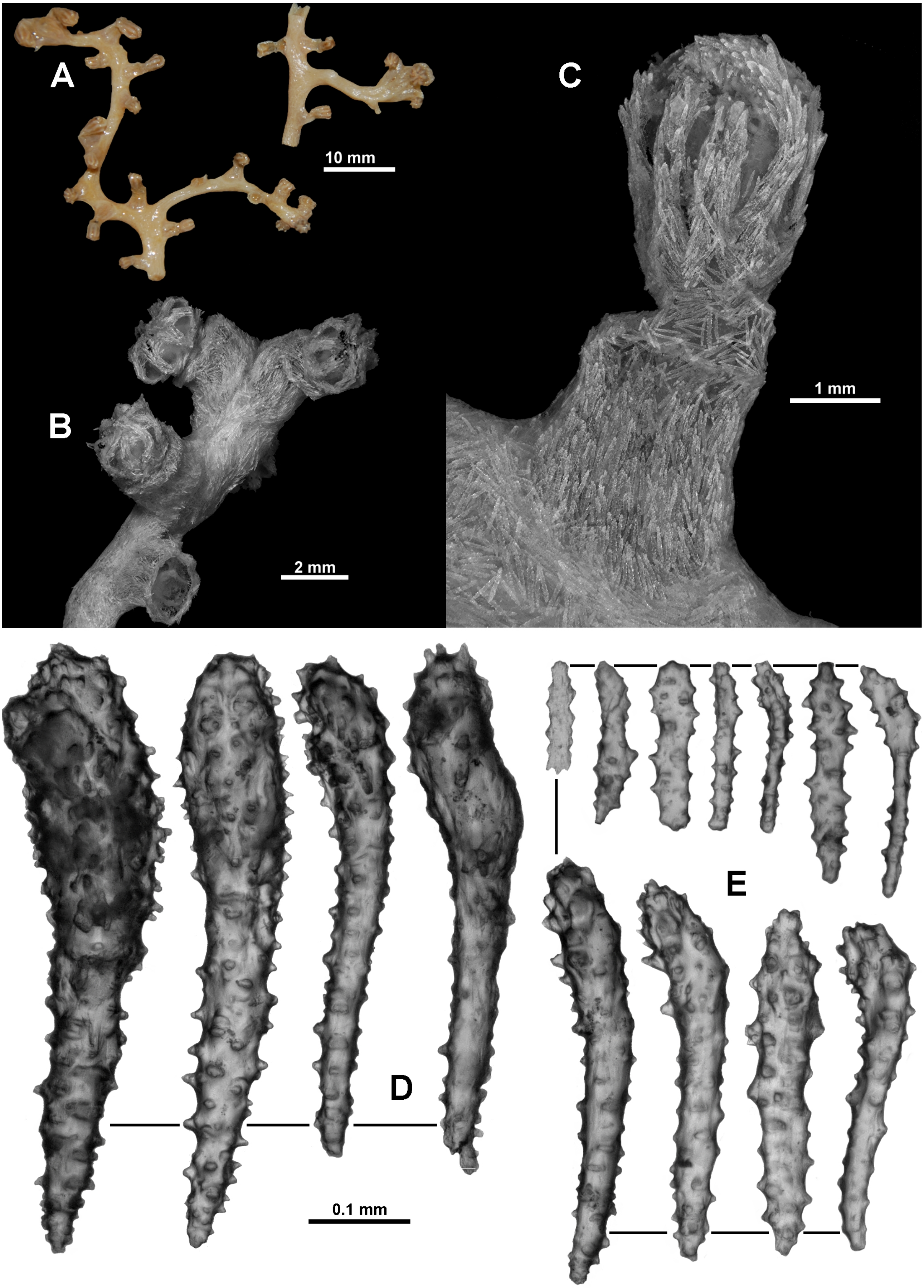

Figure 2.76. *Victorgorgia argentea* (Studer, 1894), MCZ 51046: A. Colony; B. Polyp bunch; C. Extended polyp; D. Point sclerites; E. Pinnule and tentacle rachis sclerites.

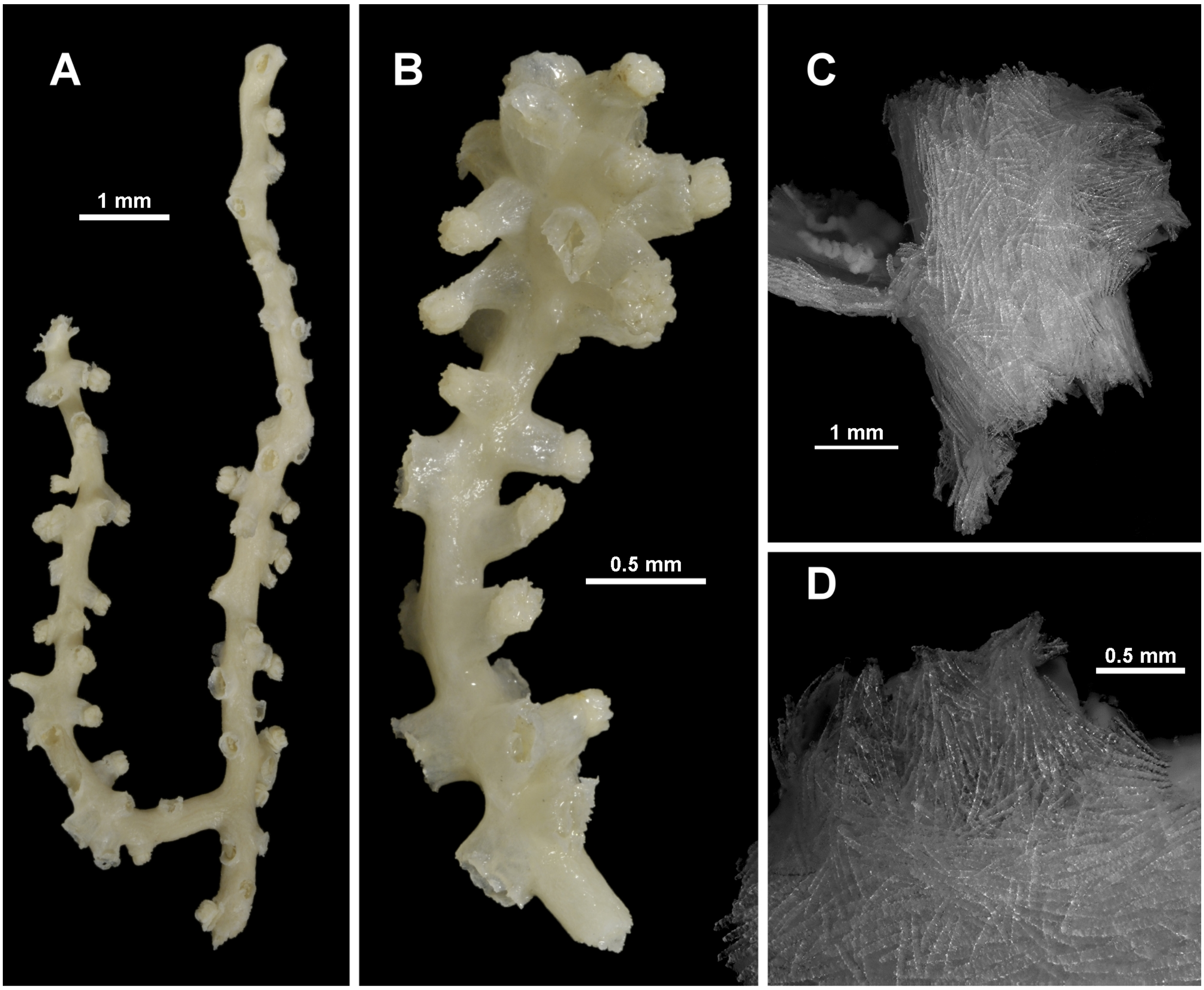

Figure 2.77. *Victorgorgia alba* (Nutting, 1908), holotype: A-B. Colony fragments; C. Fragment examined; D. Calyx. (A-B. Courtesy of NMNH, Dr R. Ford).

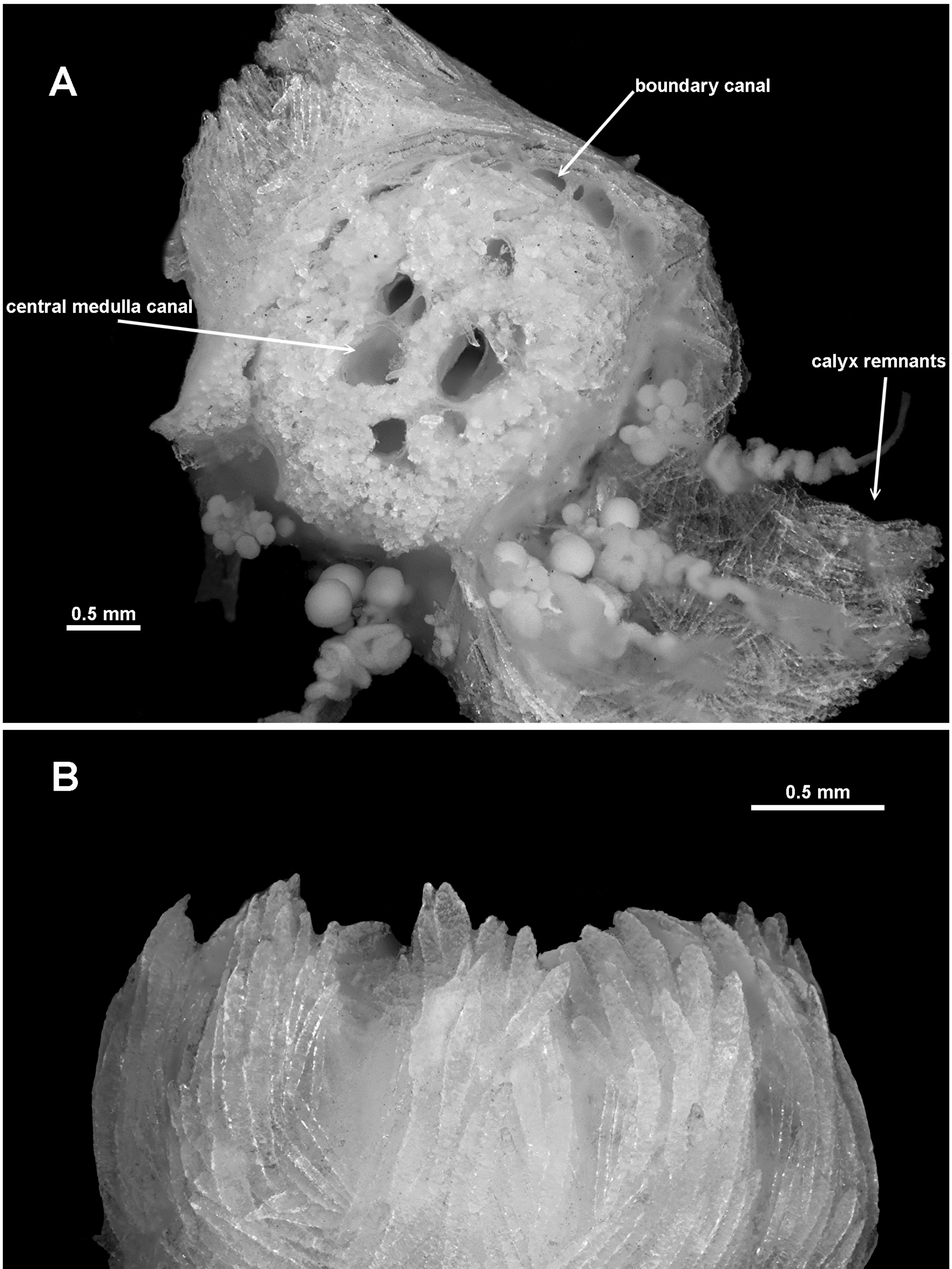

Figure 2.78. *Victorgorgia alba* (Nutting, 1908), holotype: A. Cross-section of medulla; B. Polyp head.

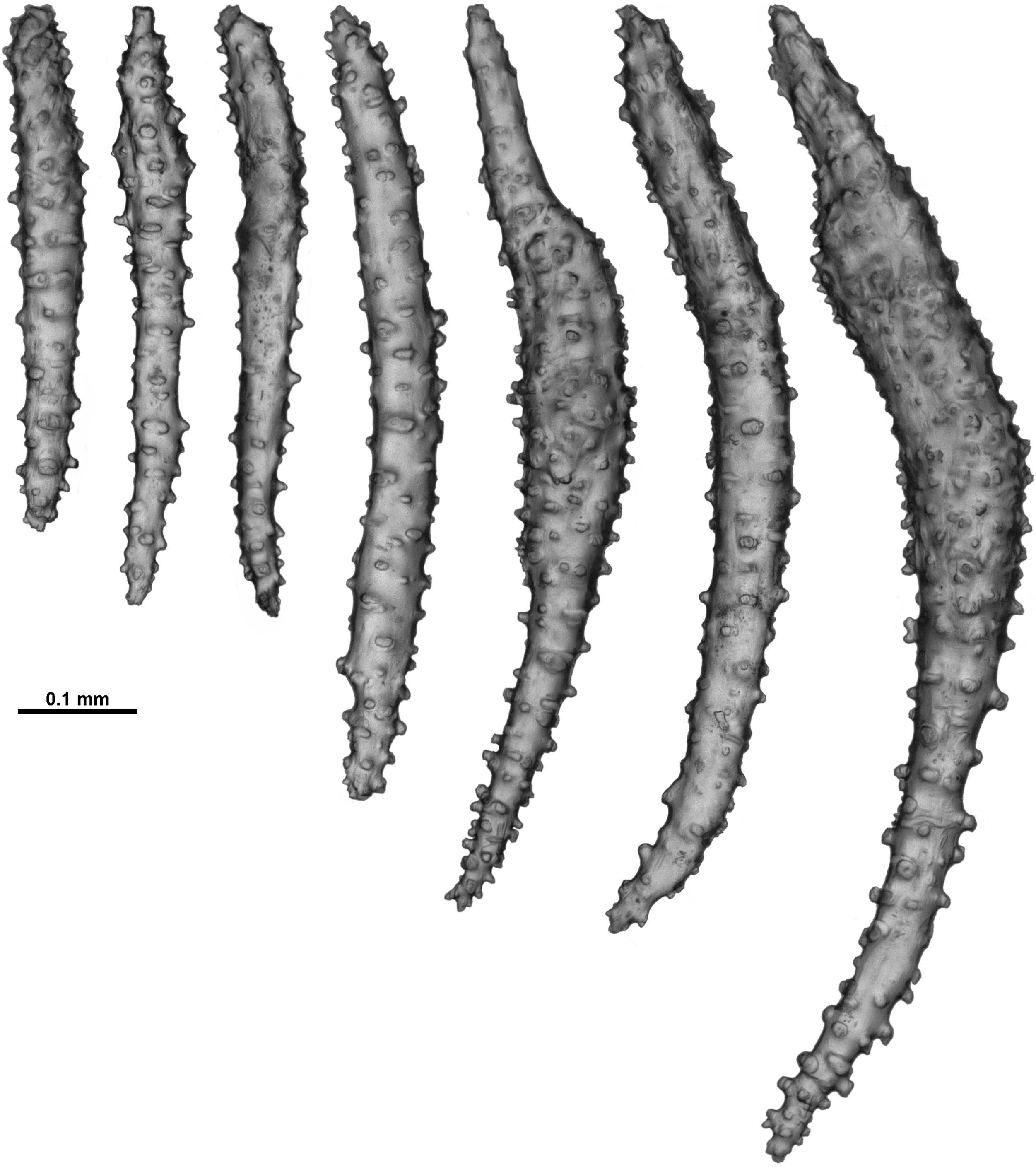

Figure 2.79. *Victorgorgia alba* (Nutting, 1908), holotype, sclerites: Collaret and point.

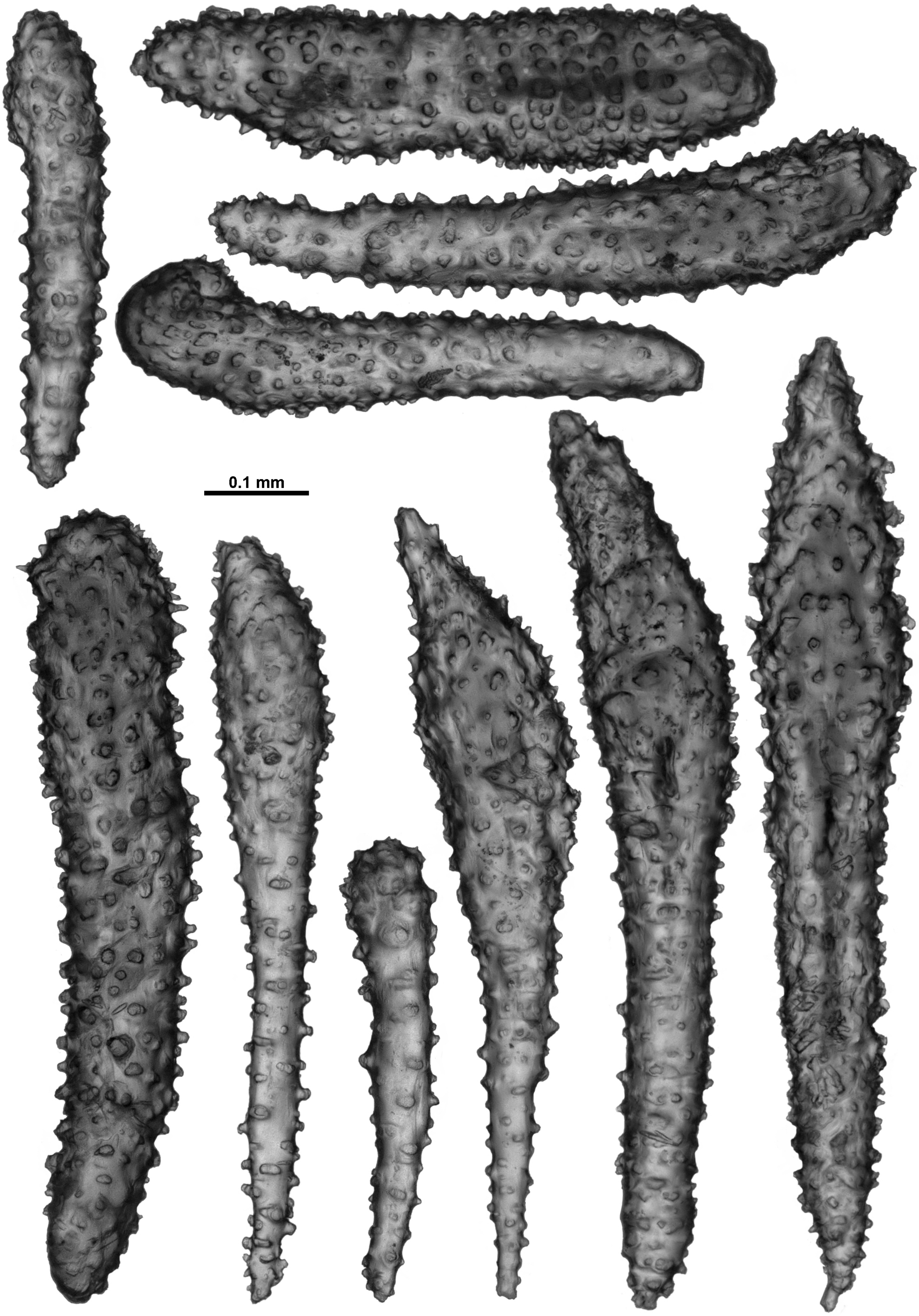

Figure 2.80. *Victorgorgia alba* (Nutting, 1908), holotype: Large point sclerites.

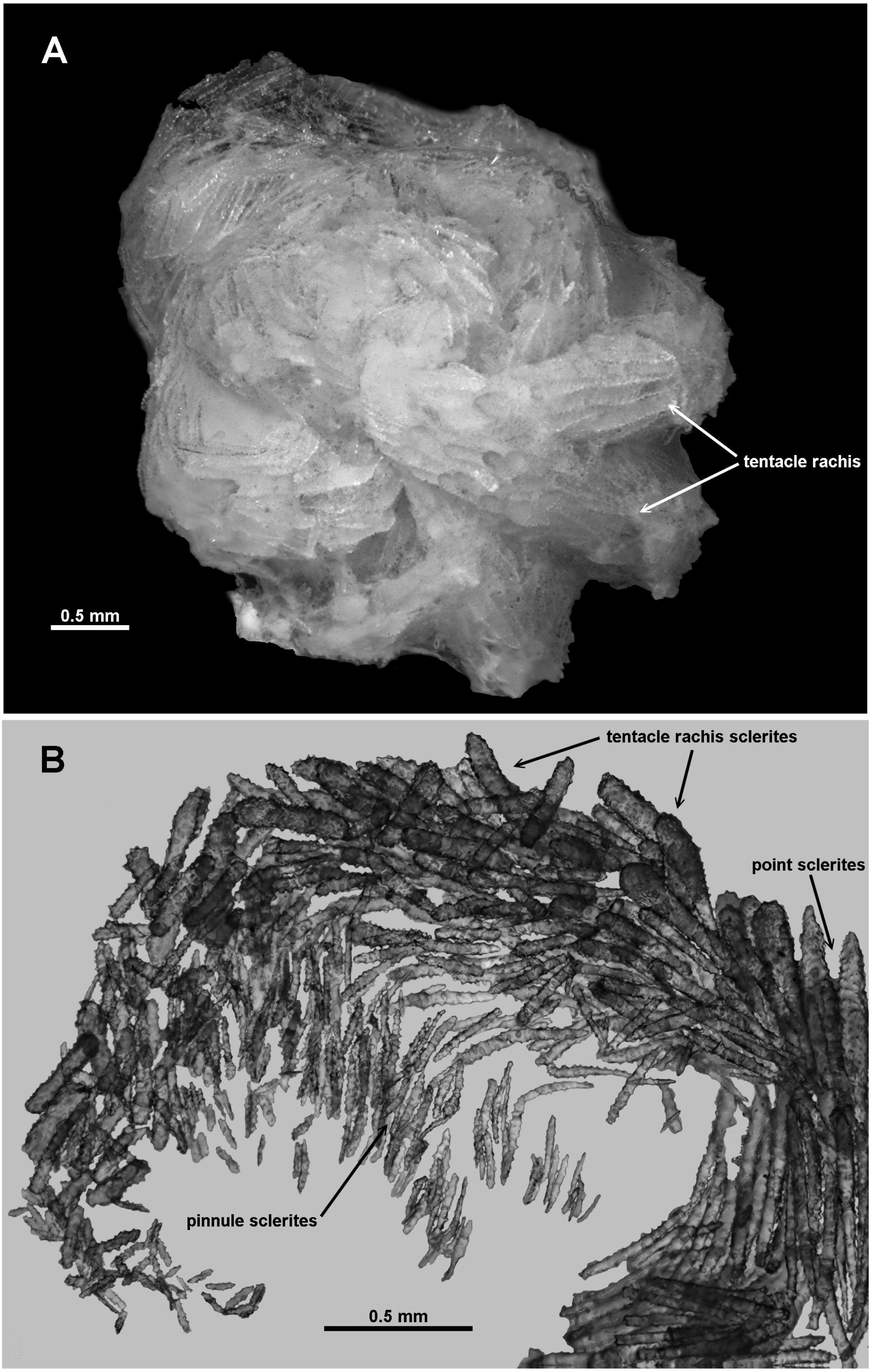

Figure 2.81. *Victorgorgia alba* (Nutting, 1908), holotype: A. Tentacles folded over polyp head; B. Tentacle and point sclerites in situ.

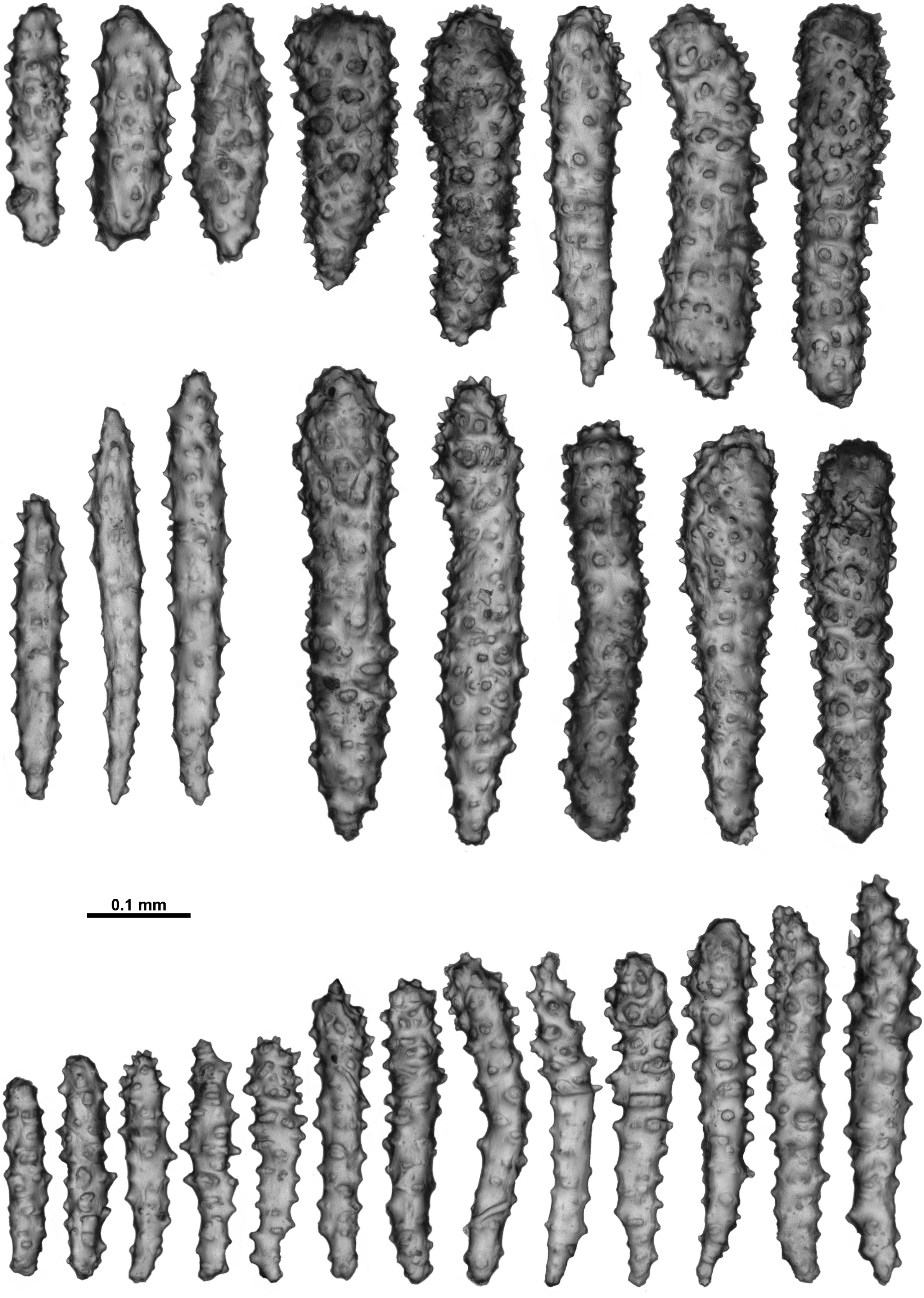

Figure 2.82. *Victorgorgia alba* (Nutting, 1908), holotype, sclerites: Tentacle rachis.

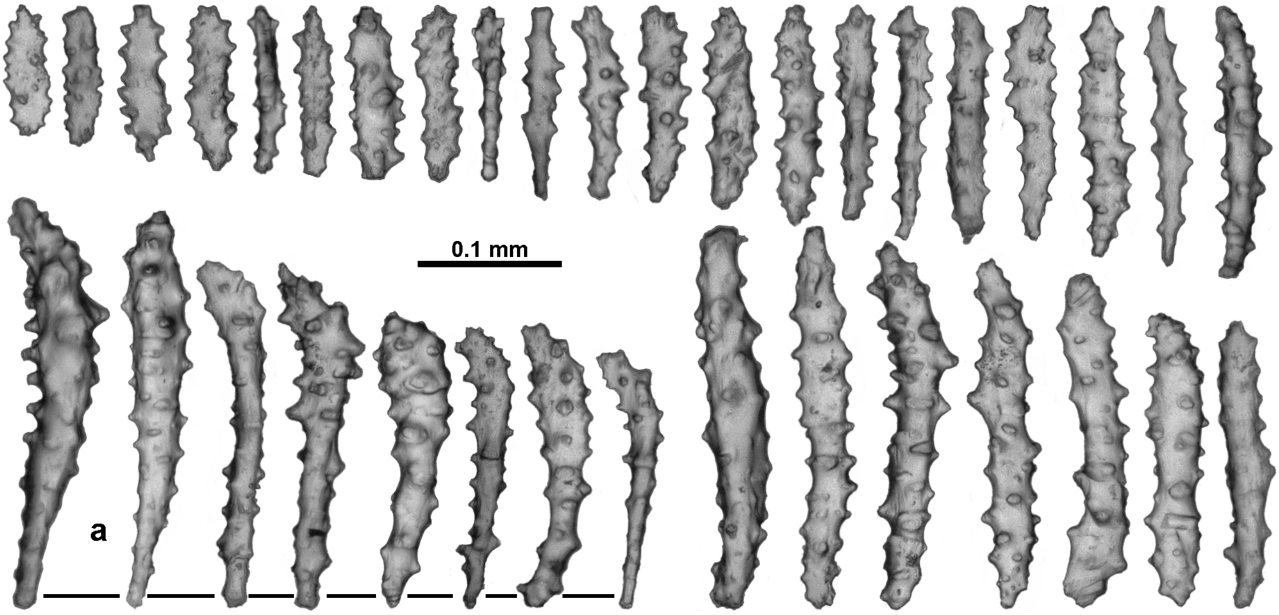

Figure 2.83. *Victorgorgia alba* (Nutting, 1908), holotype, sclerites: Pinnule (a. poorly developed josephinae clubs).

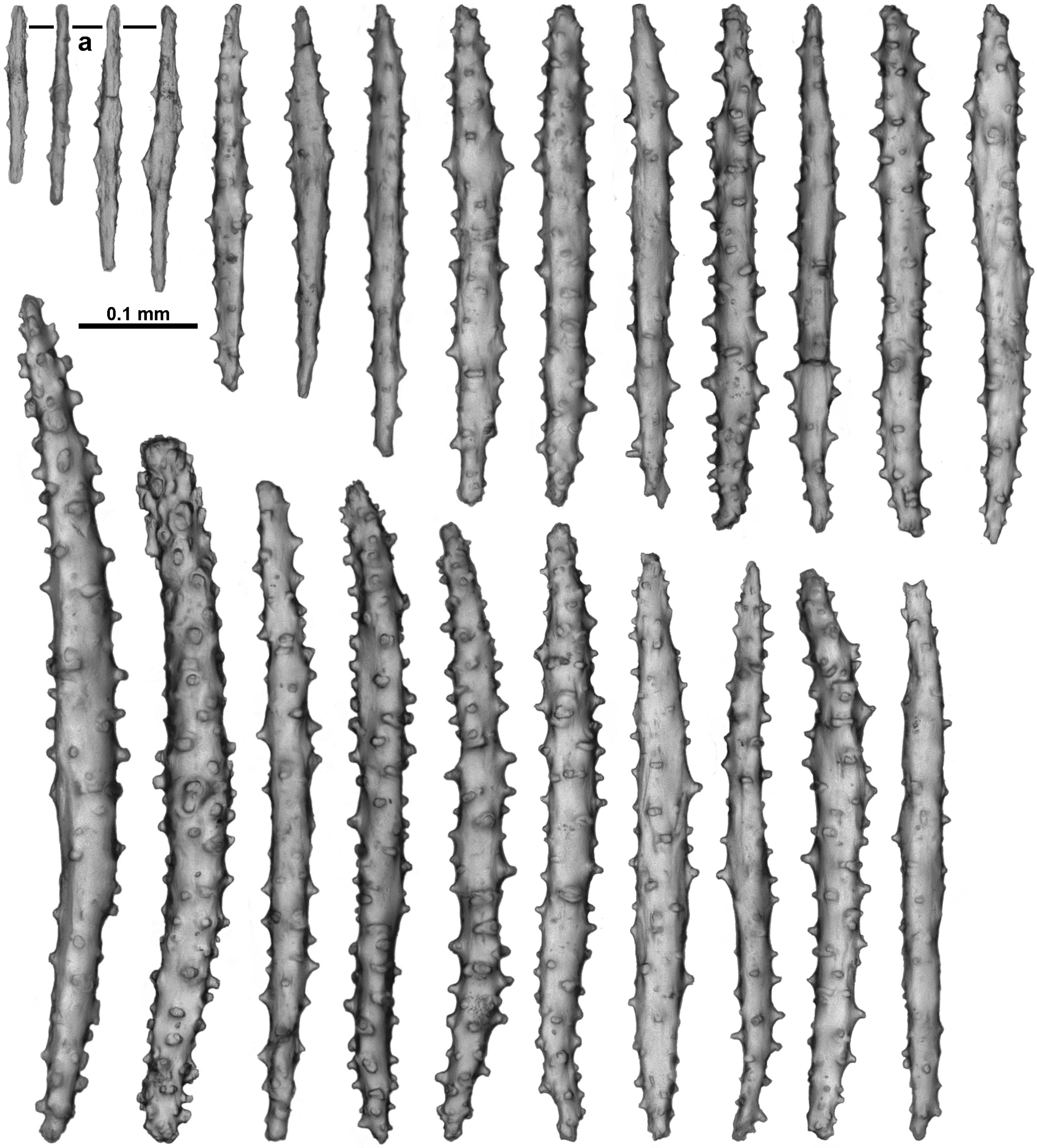

Figure 2.84. *Victorgorgia alba* (Nutting, 1908), holotype, sclerites: Calyx (a. flanged spindles).

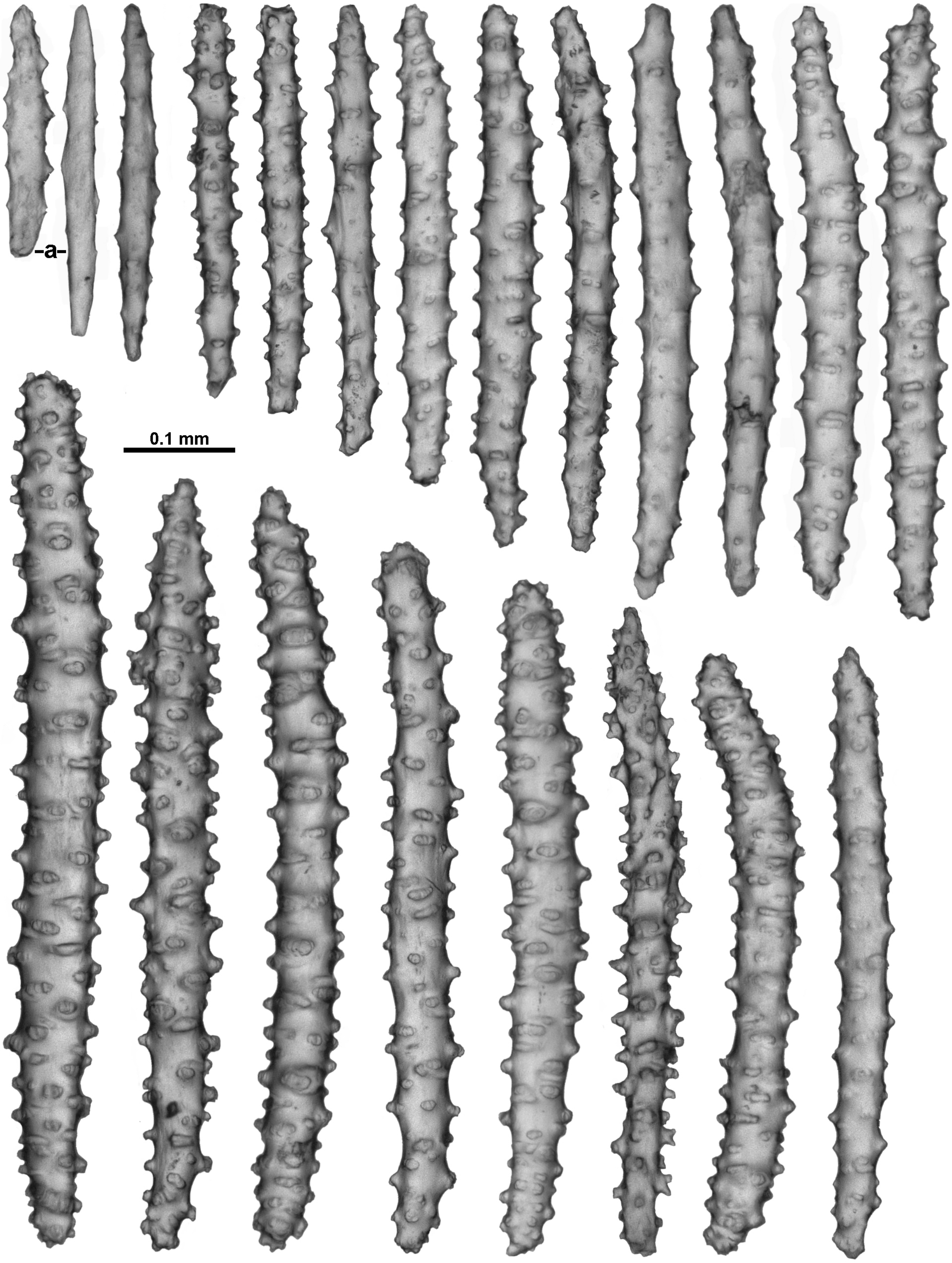

Figure 2.85. *Victorgorgia alba* (Nutting, 1908), holotype, sclerites: Cortex (a. flanged spindles).

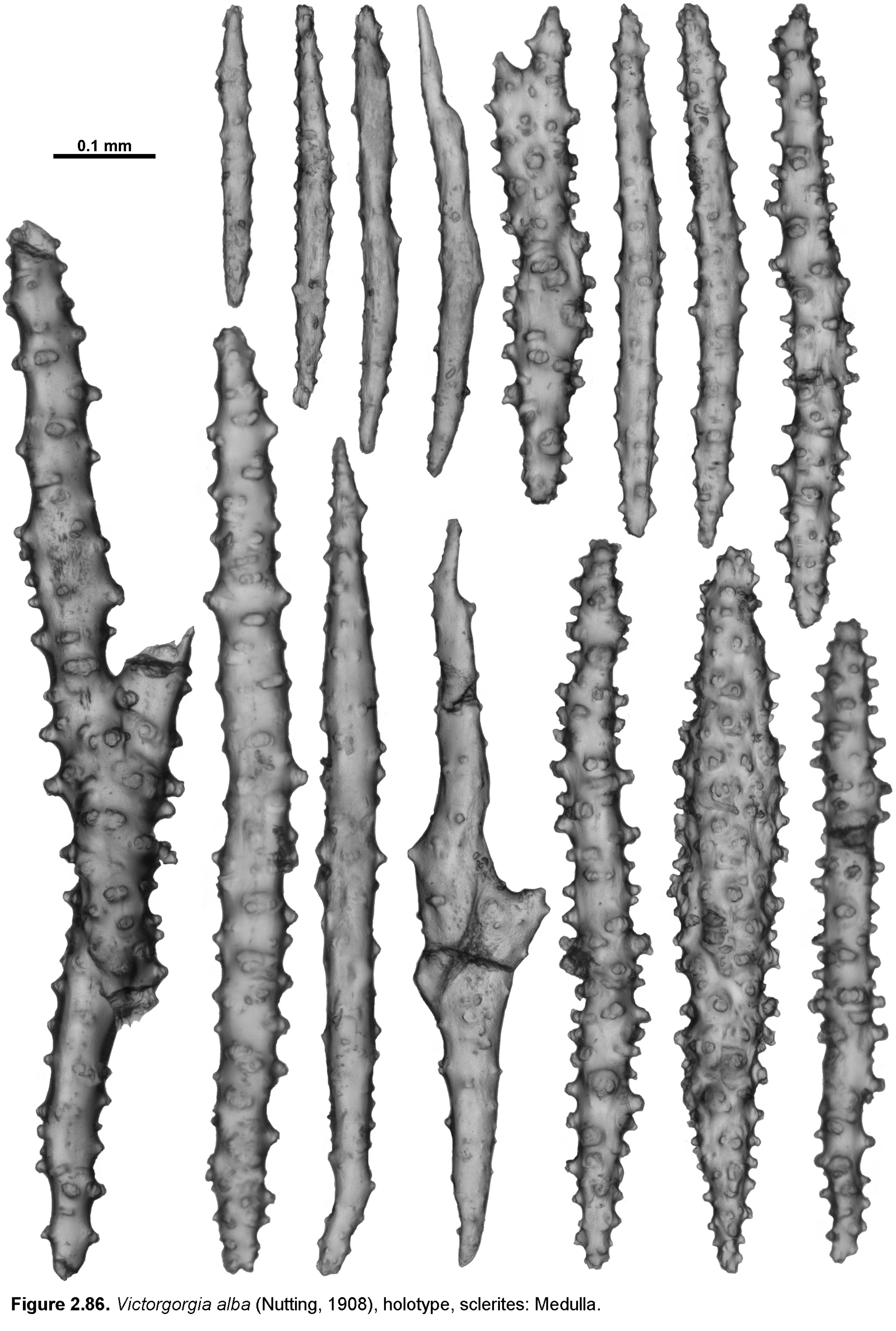

Figure 2.86. *Victorgorgia alba* (Nutting, 1908), holotype, sclerites: Medulla.

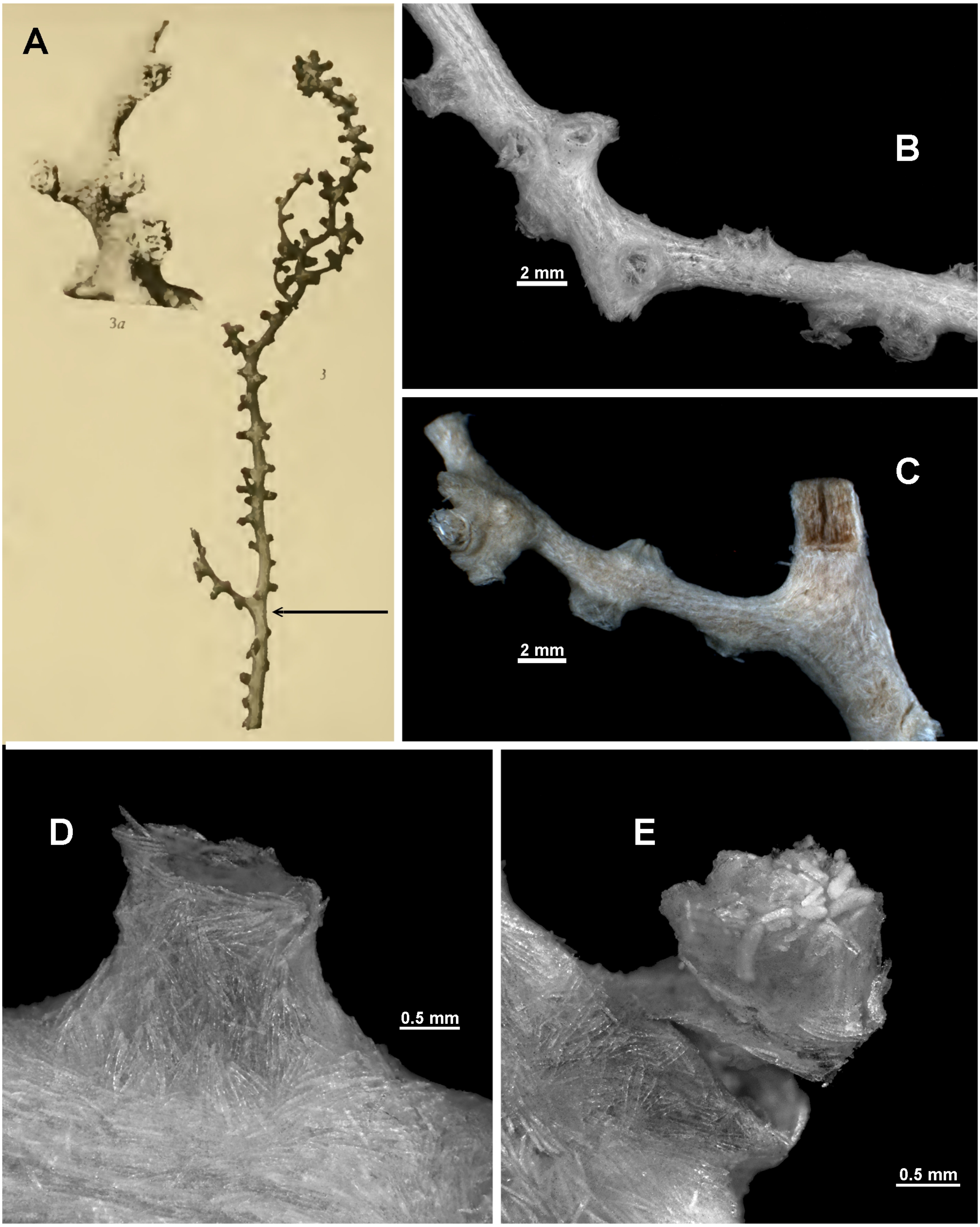

Figure 2.87. *Victorgorgia macrocalyx* (Nutting, 1911), holotype: A. Nutting's colony figure; B-C. Colony fragments; D. Calyx; E. Polyp.

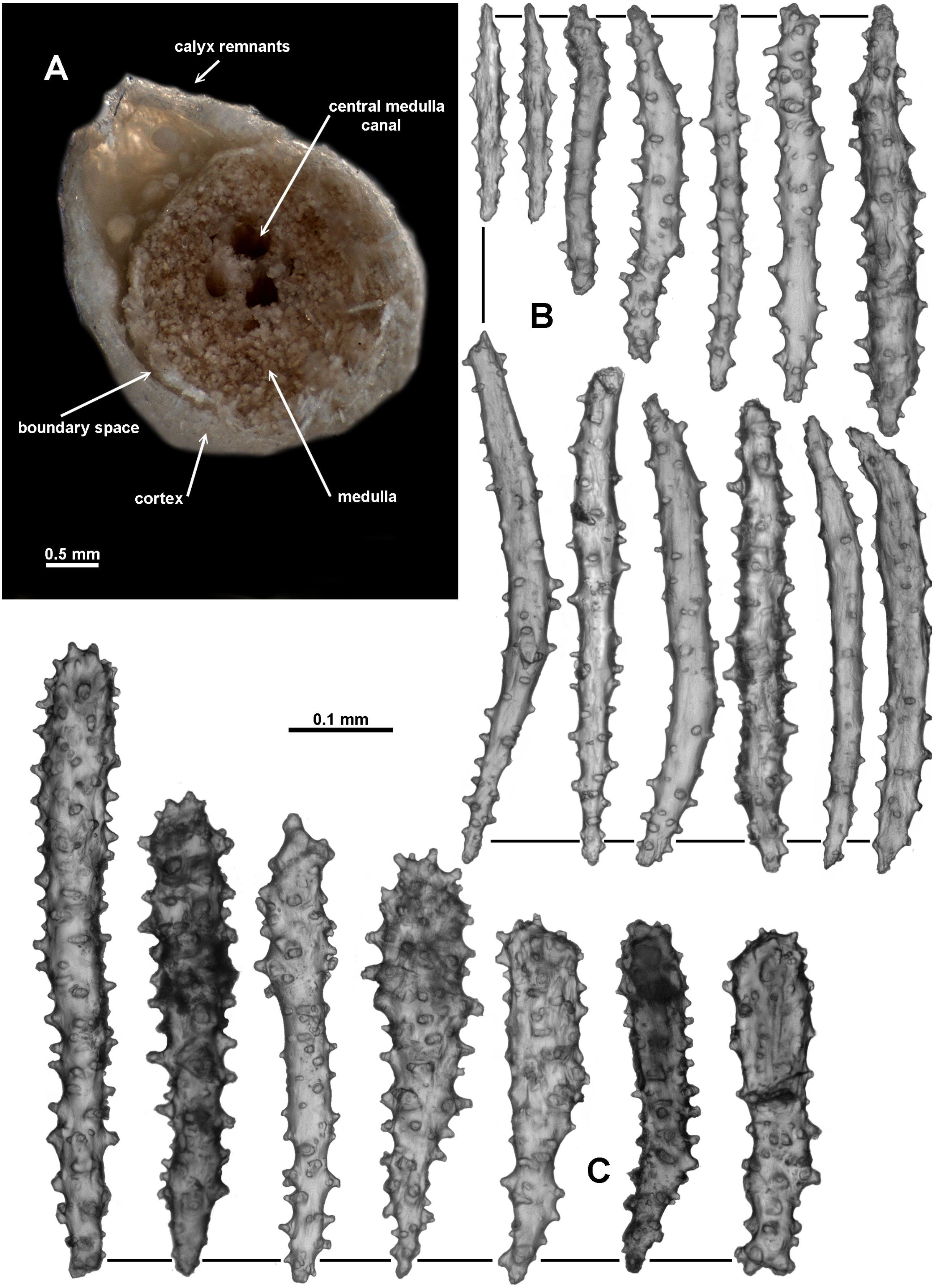

Figure 2.88. *Victorgorgia macrocalyx* (Nutting, 1911), holotype: A. Cross-section of axis; B. Point sclerites; C. Clubbed point and tentacle rachis sclerites.

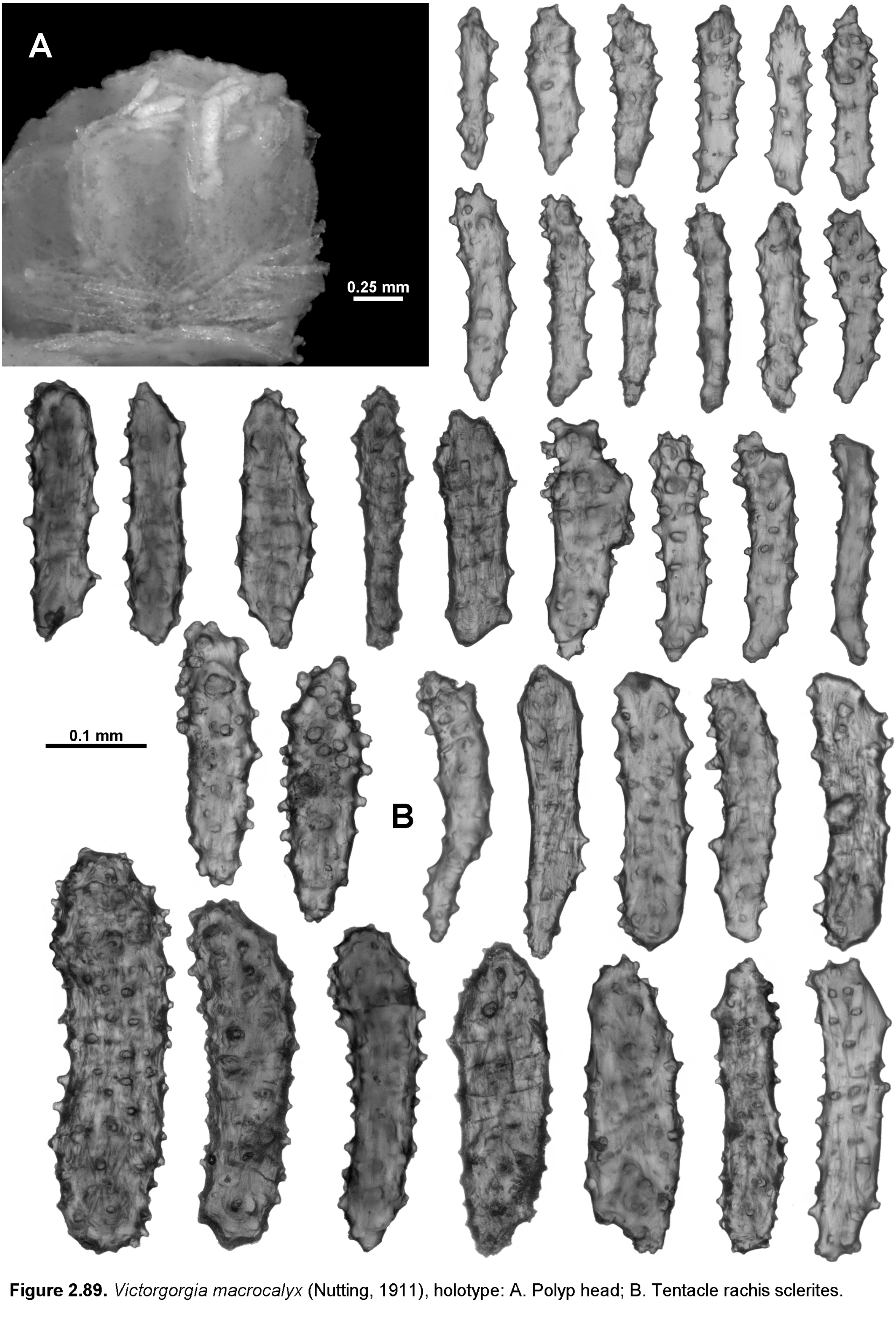

Figure 2.89. *Victorgorgia macrocalyx* (Nutting, 1911), holotype: A. Polyp head; B. Tentacle rachis sclerites.

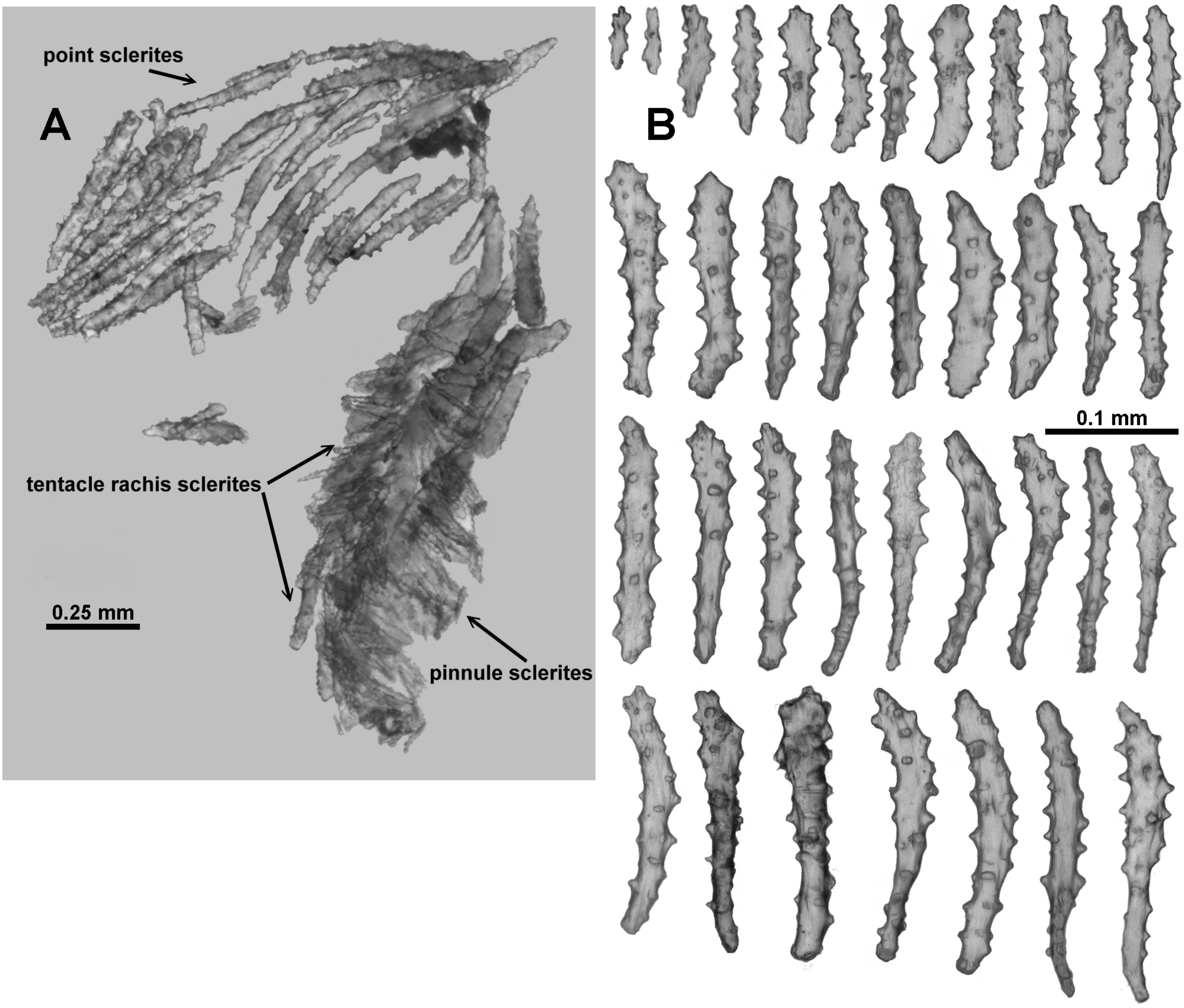

Figure 2.90. *Victorgorgia macrocalyx* (Nutting, 1911), holotype: A. Tentacle and point sclerites in situ; B. Pinnule sclerites.

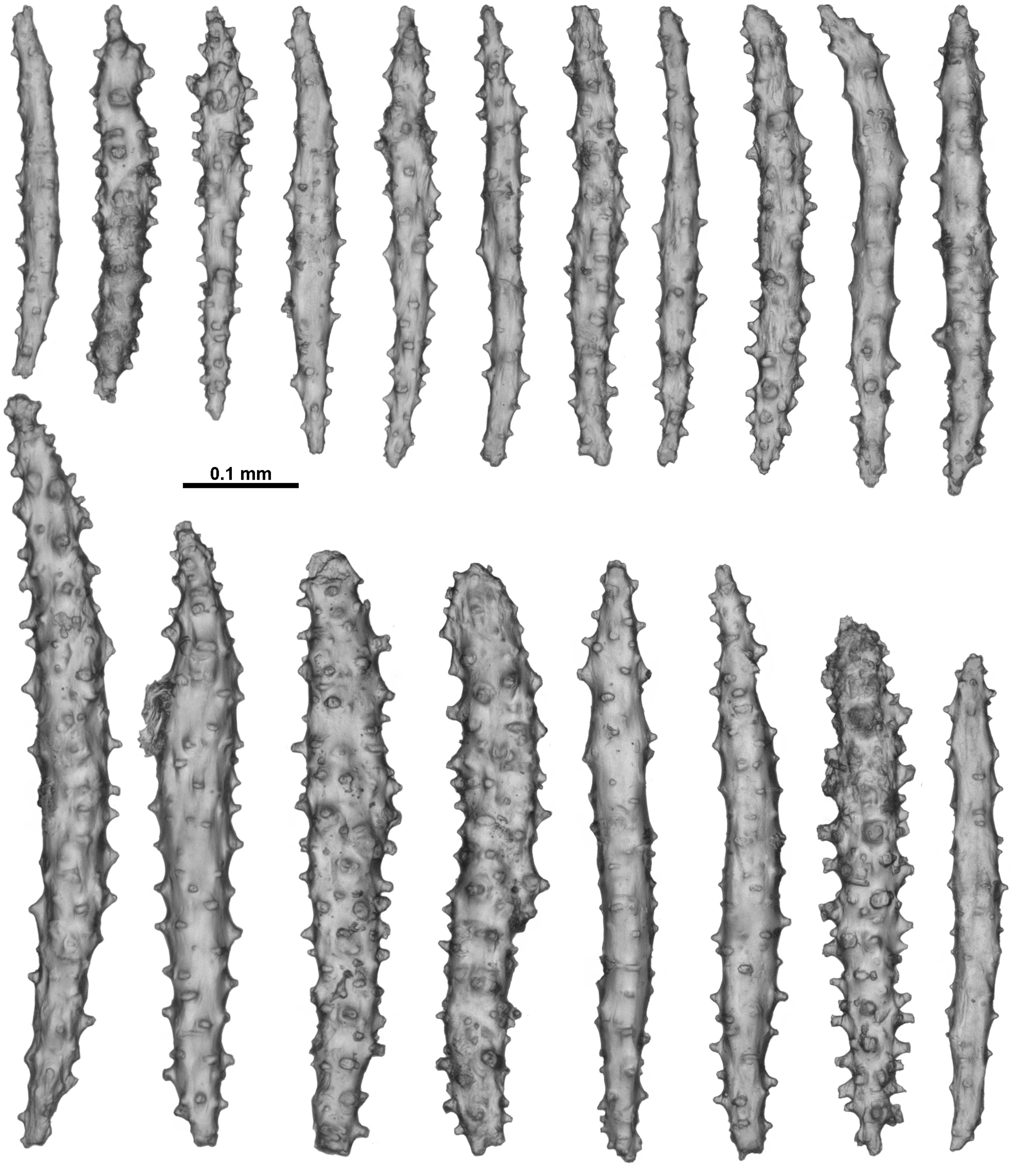

Figure 2.91. *Victorgorgia macrocalyx* (Nutting, 1911), holotype, sclerites: Calyx.

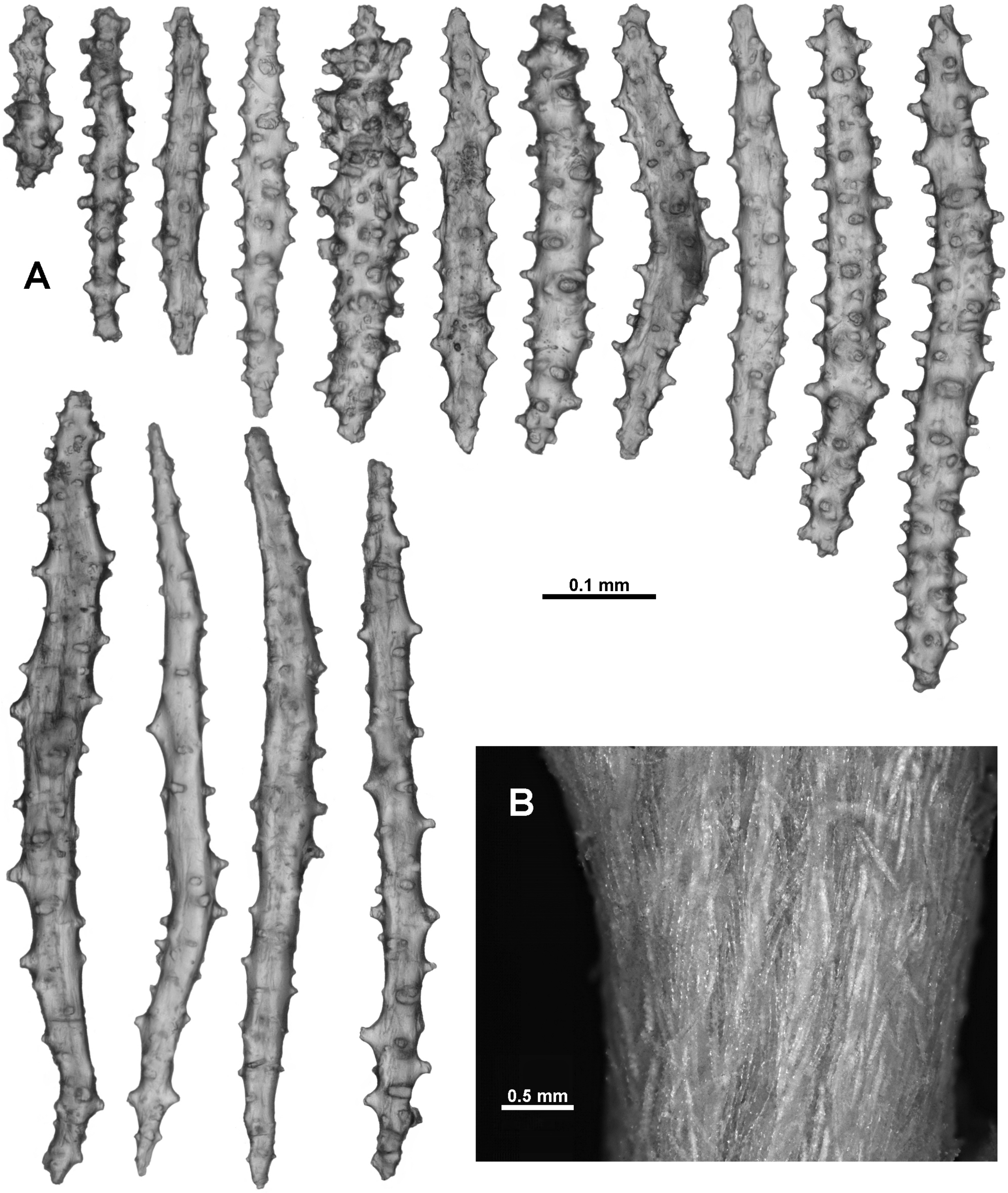

Figure 2.92. *Victorgorgia macrocalyx* (Nutting, 1911), holotype: A. Cortex sclerites; B. Colony surface with channels

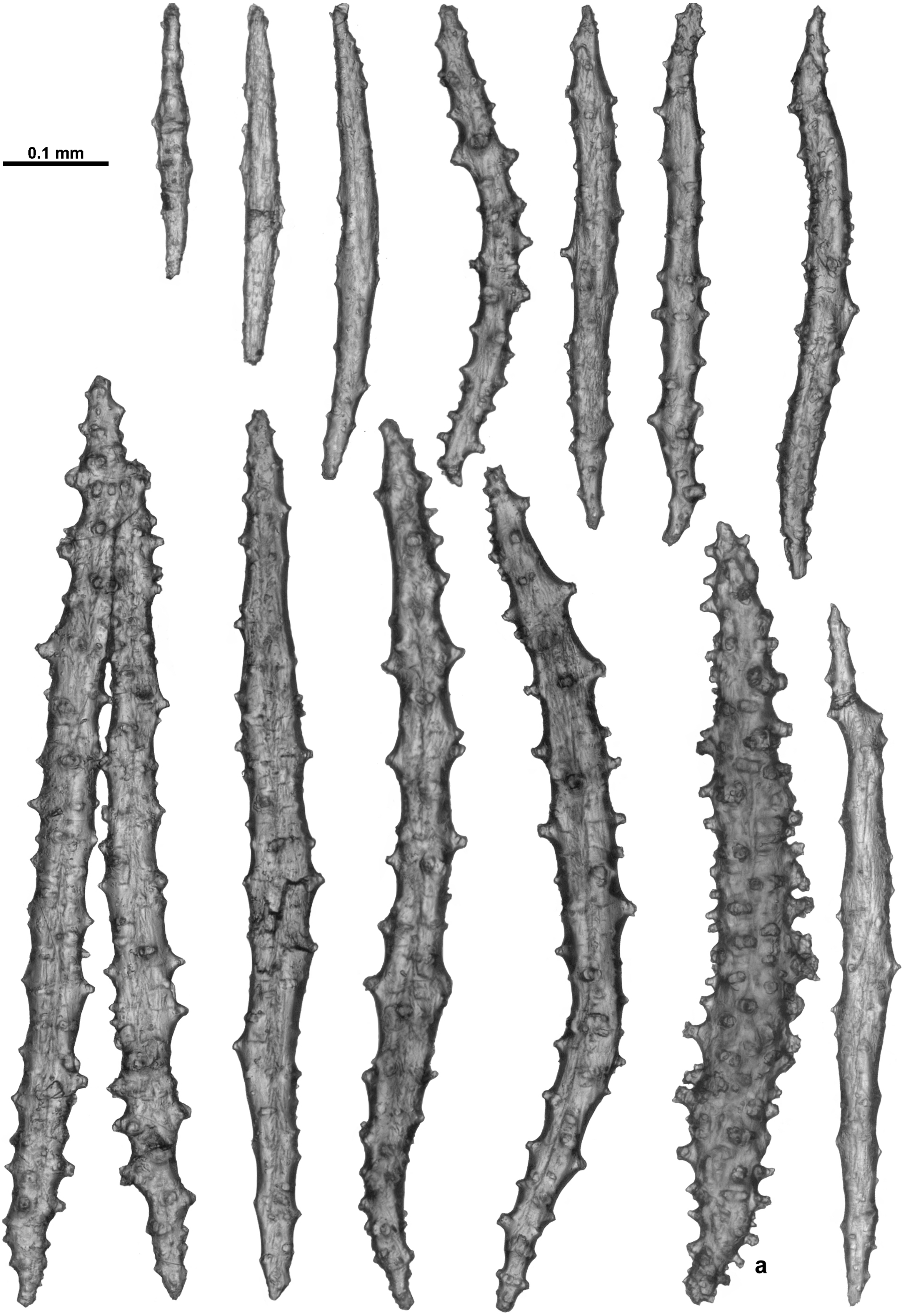

Figure 2.93. *Victorgorgia macrocalyx* (Nutting, 1911), holotype, sclerites: Medulla (a. more heavily tuberculate spindle).

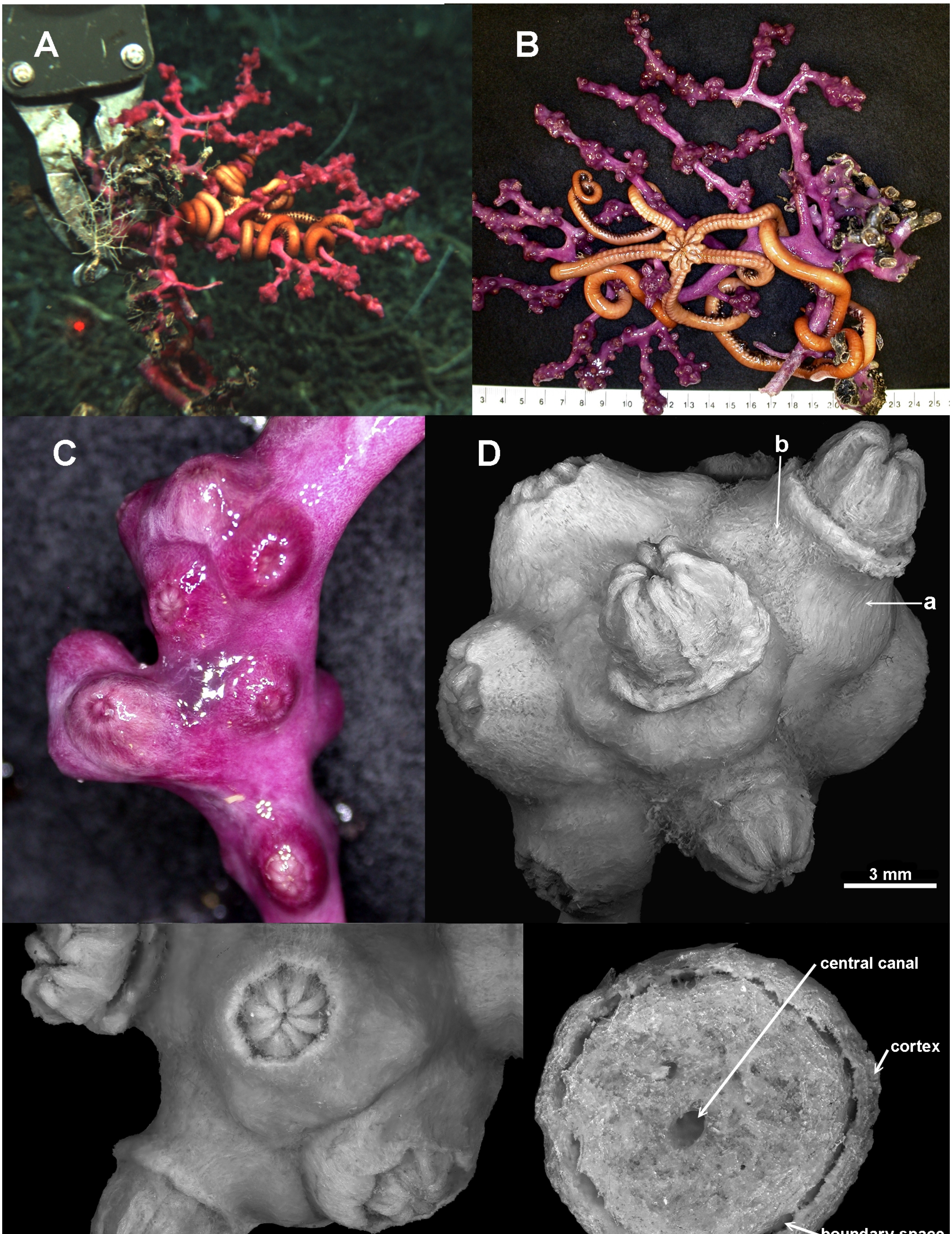

Figure 2.94. *Victorgorgia eminens*, n. sp., holotype: A. Collection of colony; B. Colony; C. Branch; D. Branch tip (a. with skin; b. skin partially removed); E. Retracted polyps; F. Cross-section of medulla. (A. Courtesy of JASON ROV, B-C. Courtesy of Karen Gowlett-Holmes, CMAR)

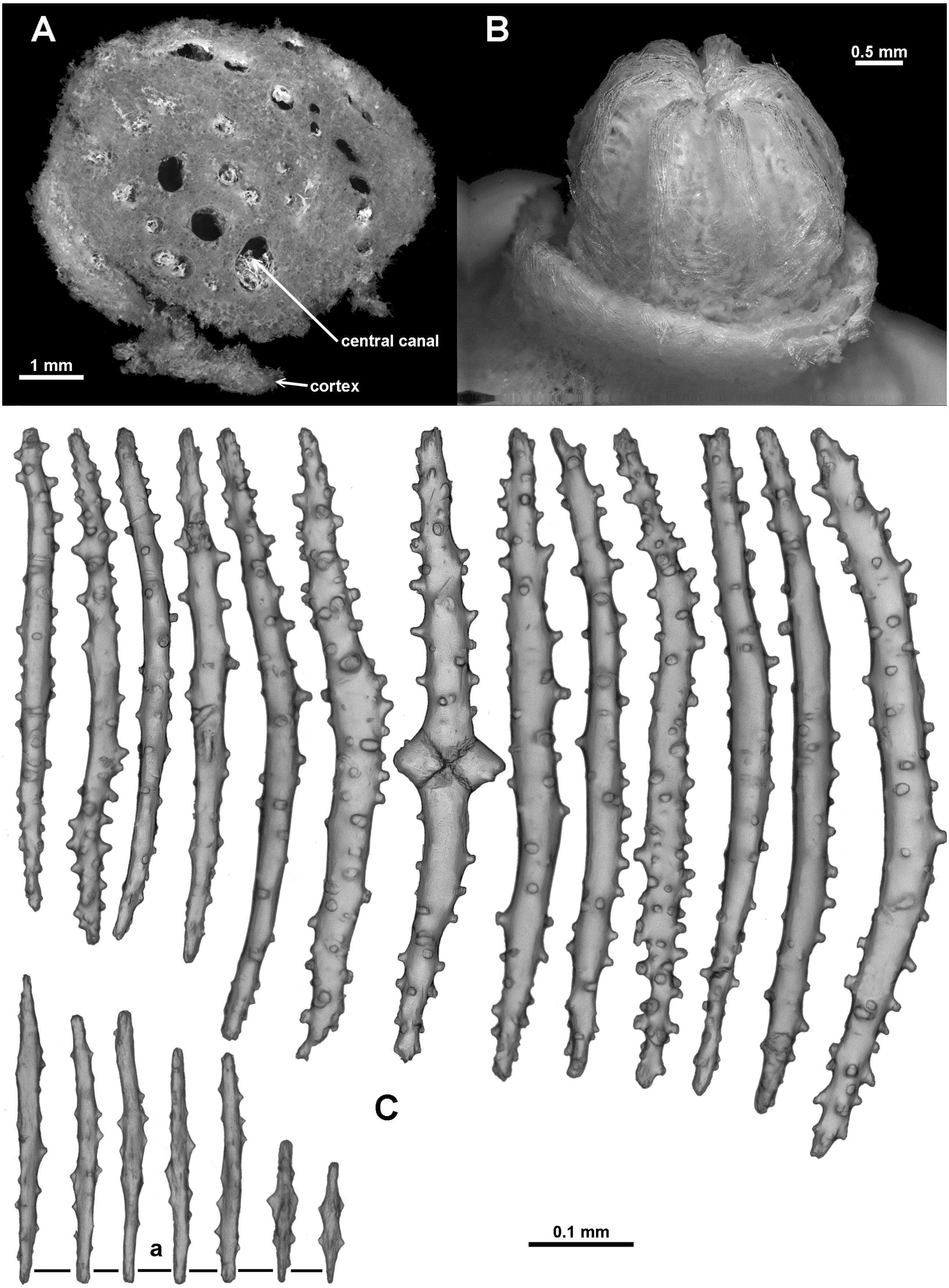

Figure 2.95. *Victorgorgia eminens,* n. sp., holotype: A. Decalcified cross-section of axis; B. Polyp head; C. Point sclerites (a. flanged spindles).

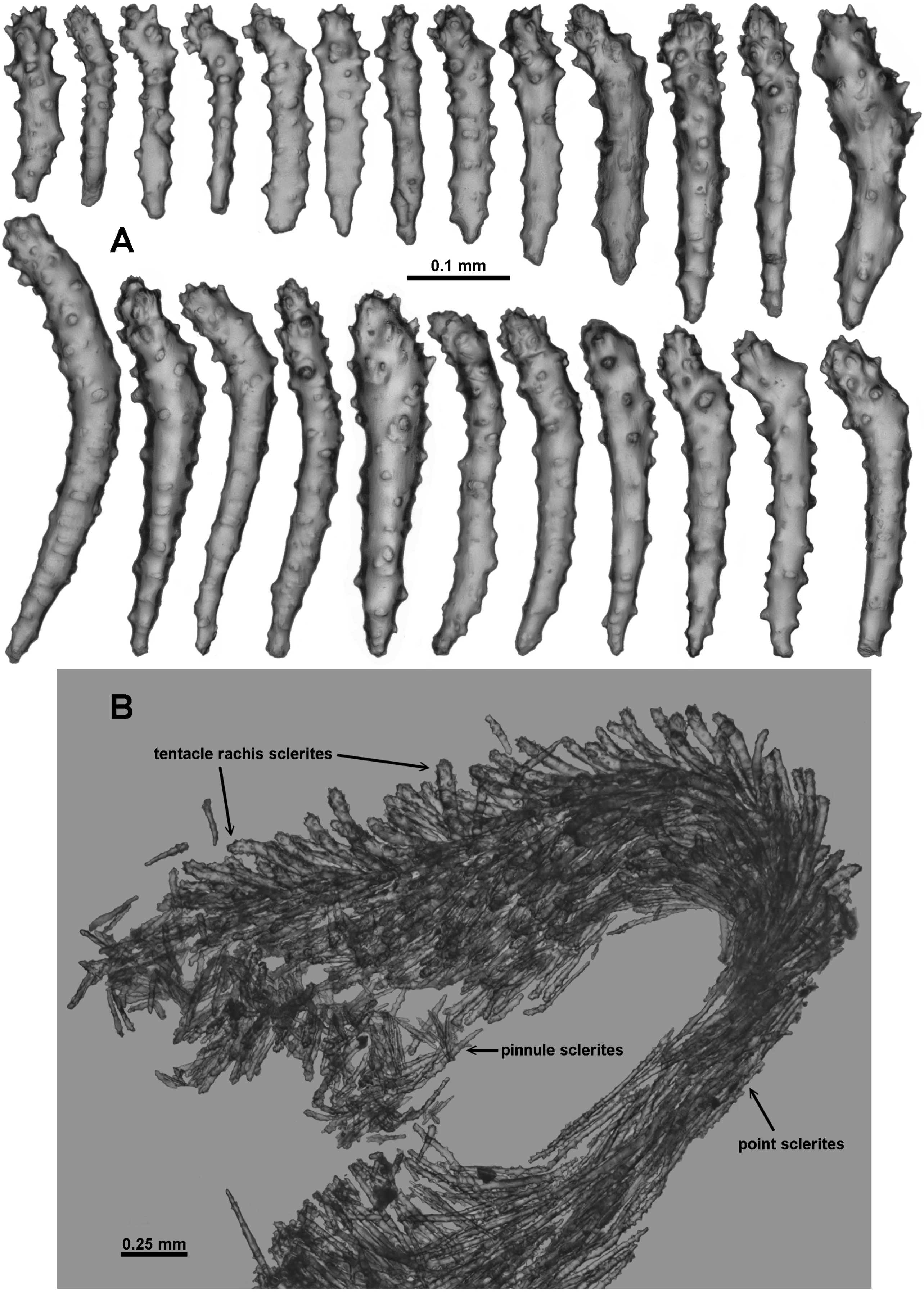

Figure 2.96. *Victorgorgia eminens,* n. sp., holotype: A. Tentacle rachis sclerites; B. Tentacle and point sclerites in situ.

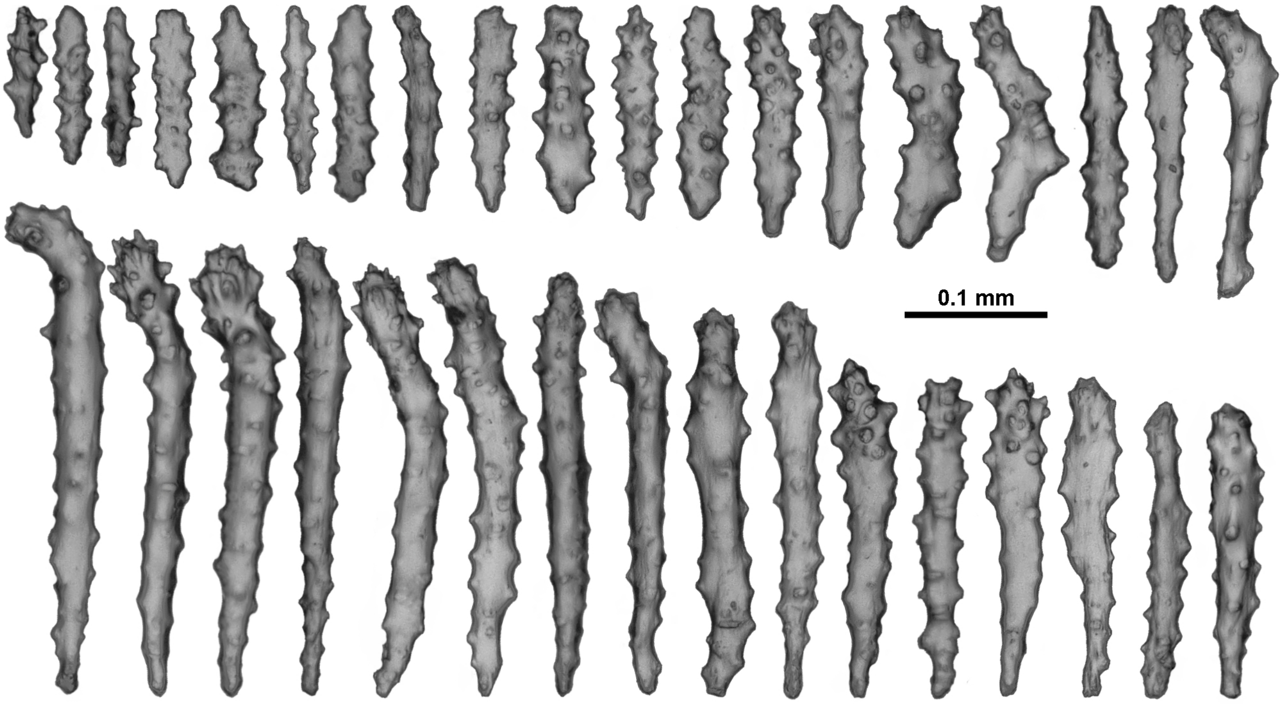

Figure 2.97. *Victorgorgia eminens,* n. sp., holotype, sclerites: Pinnule.

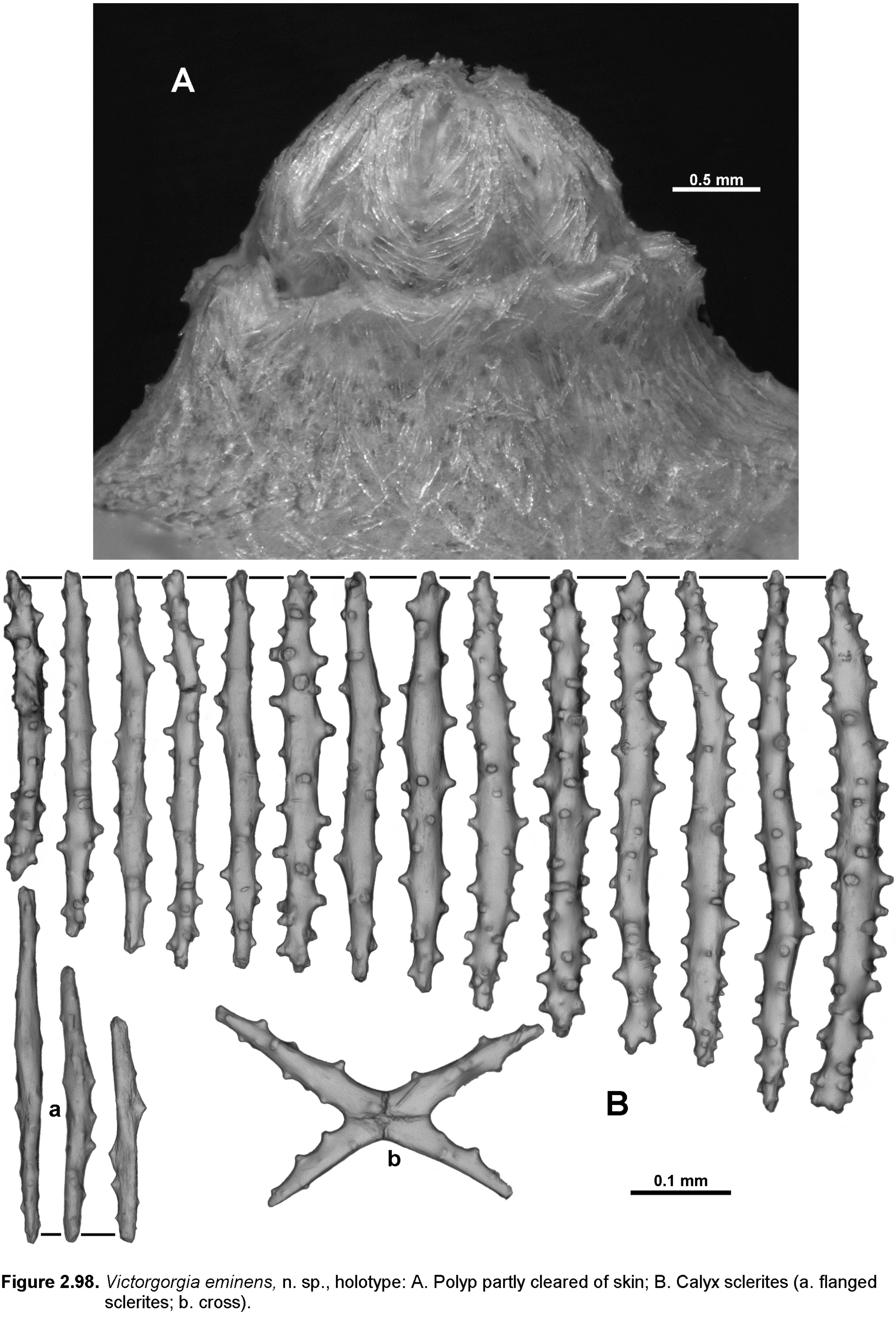

Figure 2.98. *Victorgorgia eminens,* n. sp., holotype: A. Polyp partly cleared of skin; B. Calyx sclerites (a. flanged sclerites; b. cross).

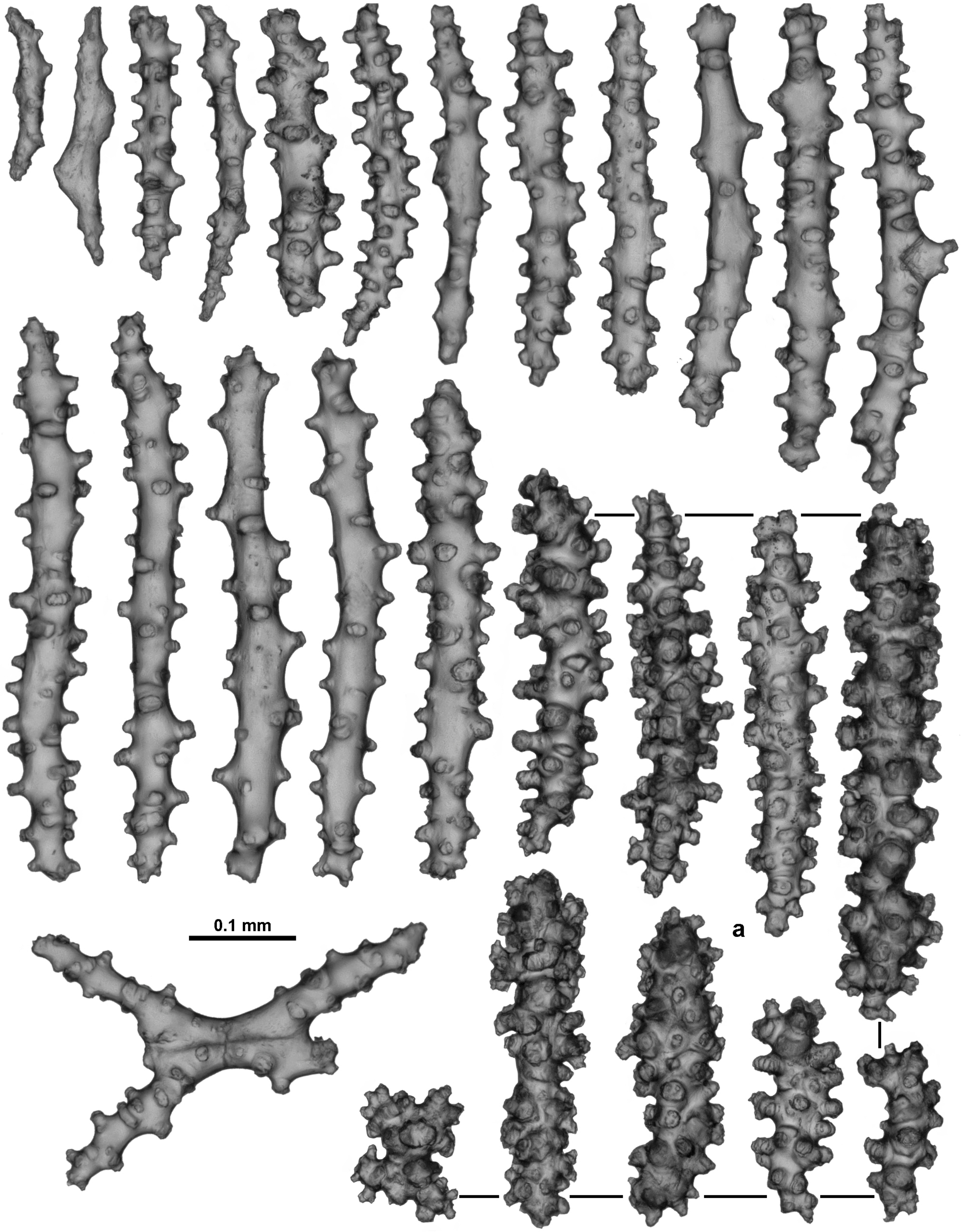

Figure 2.99. *Victorgorgia eminens,* n. sp., holotype, sclerites: Cortex (a. more heavily tuberculate sclerites).

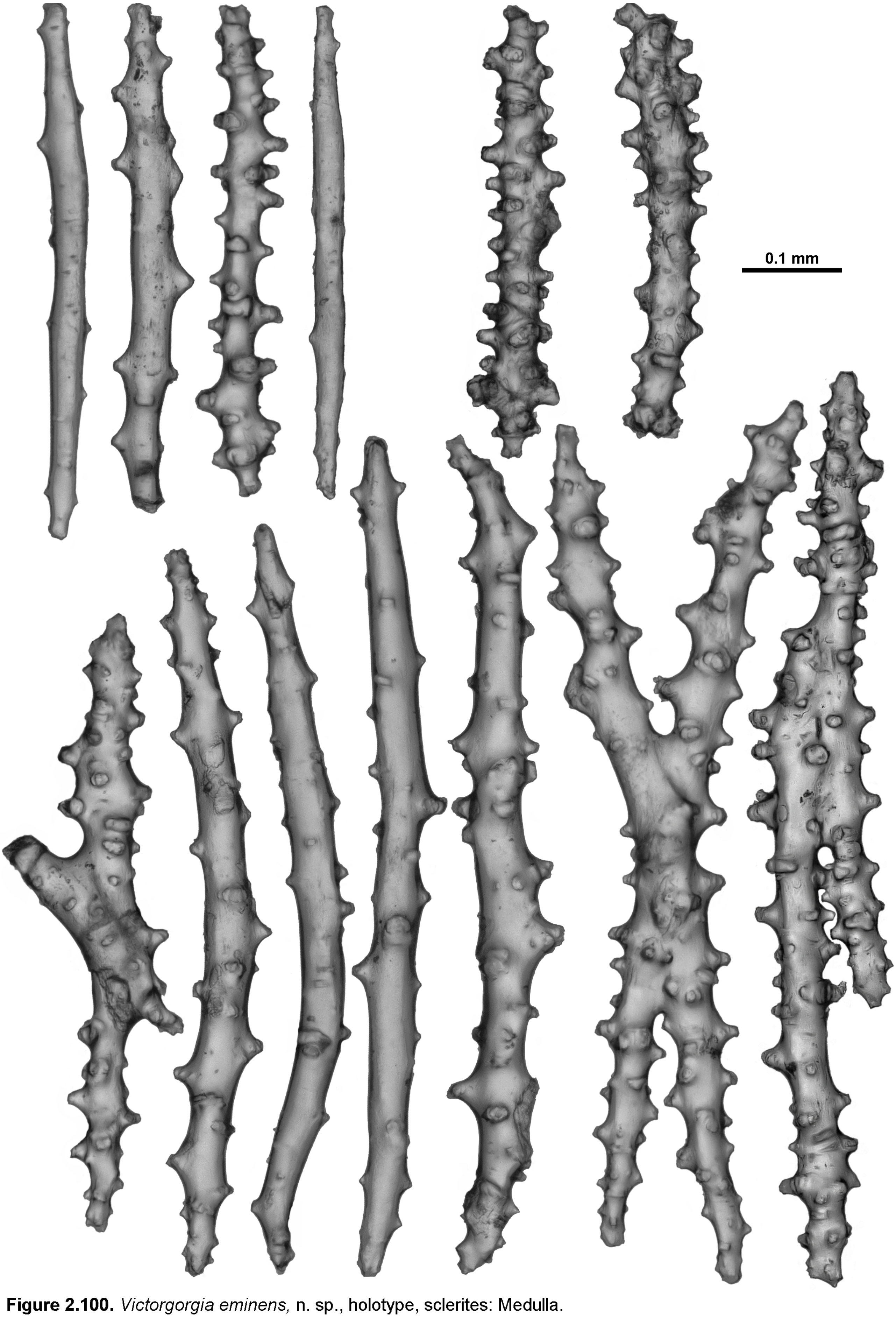

Figure 2.100. *Victorgorgia eminens,* n. sp., holotype, sclerites: Medulla.

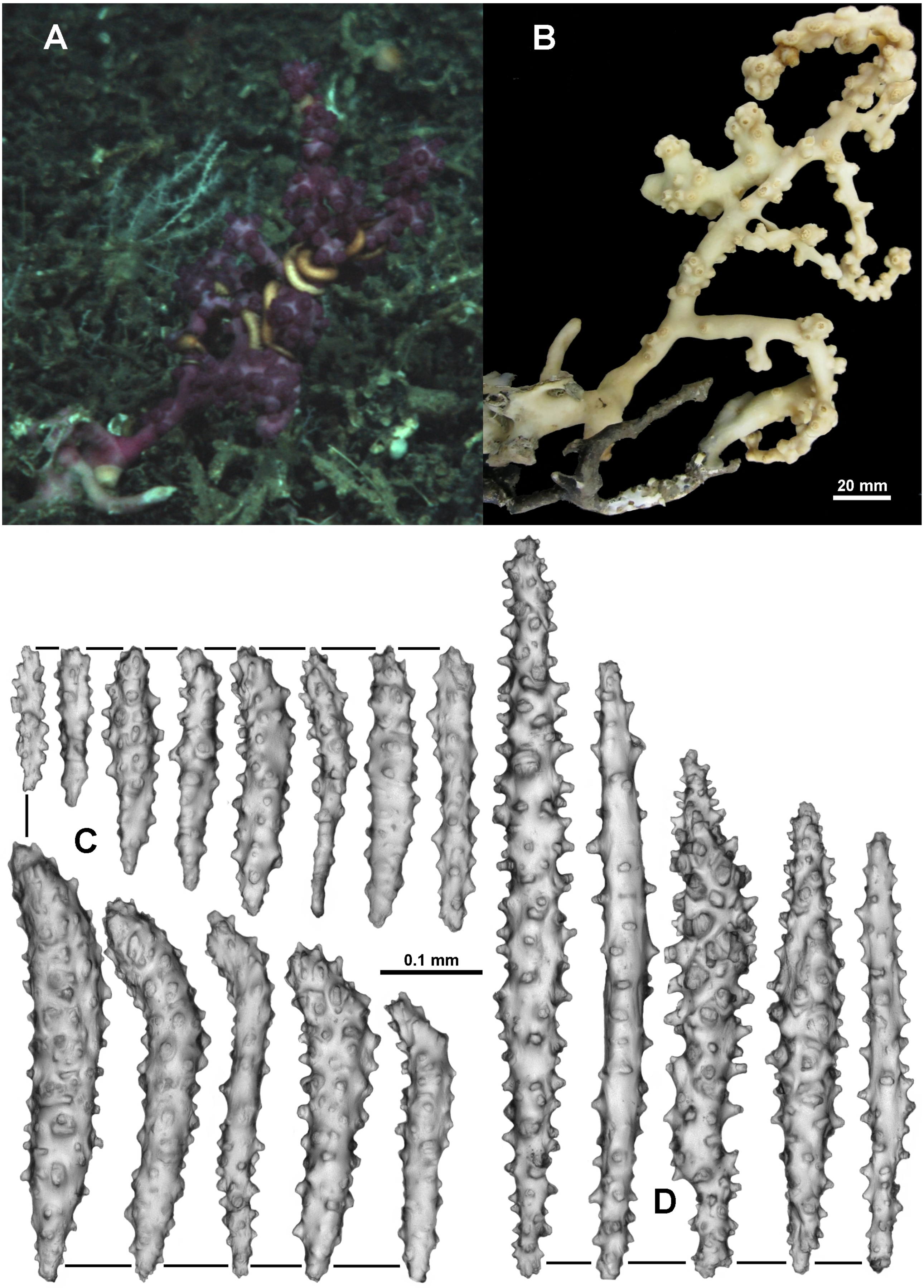

Figure 2.101. *Victorgorgia eminens,* n. sp., TMAG K4267: A. Colony in situ; B. Preserved colony; C. Tentacle rachis sclerites; D. Calyx sclerites. (A. Courtesy of JASON ROV).

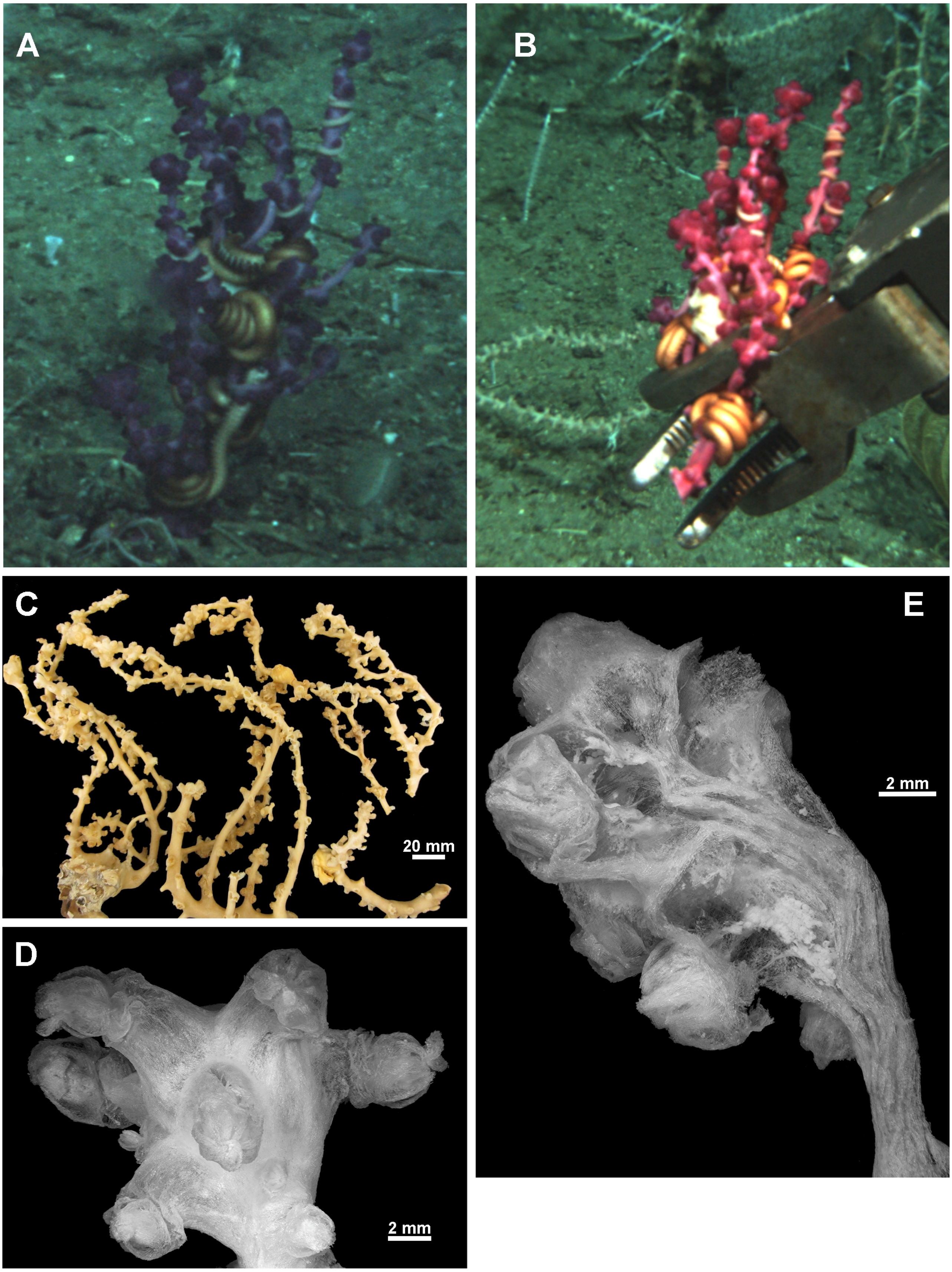

Figure 2.102. *Victorgorgia eminens,* n. sp.: A-B. TMAG K4268: (A). Colony in situ in muted light; (B). Colony in bright light. C-E. TMAG K4271: (C). Preserved colony; (D). Exert polyps; (E). Longitudinal cross-section of branch tip. (A-B. Courtesy of JASON ROV).

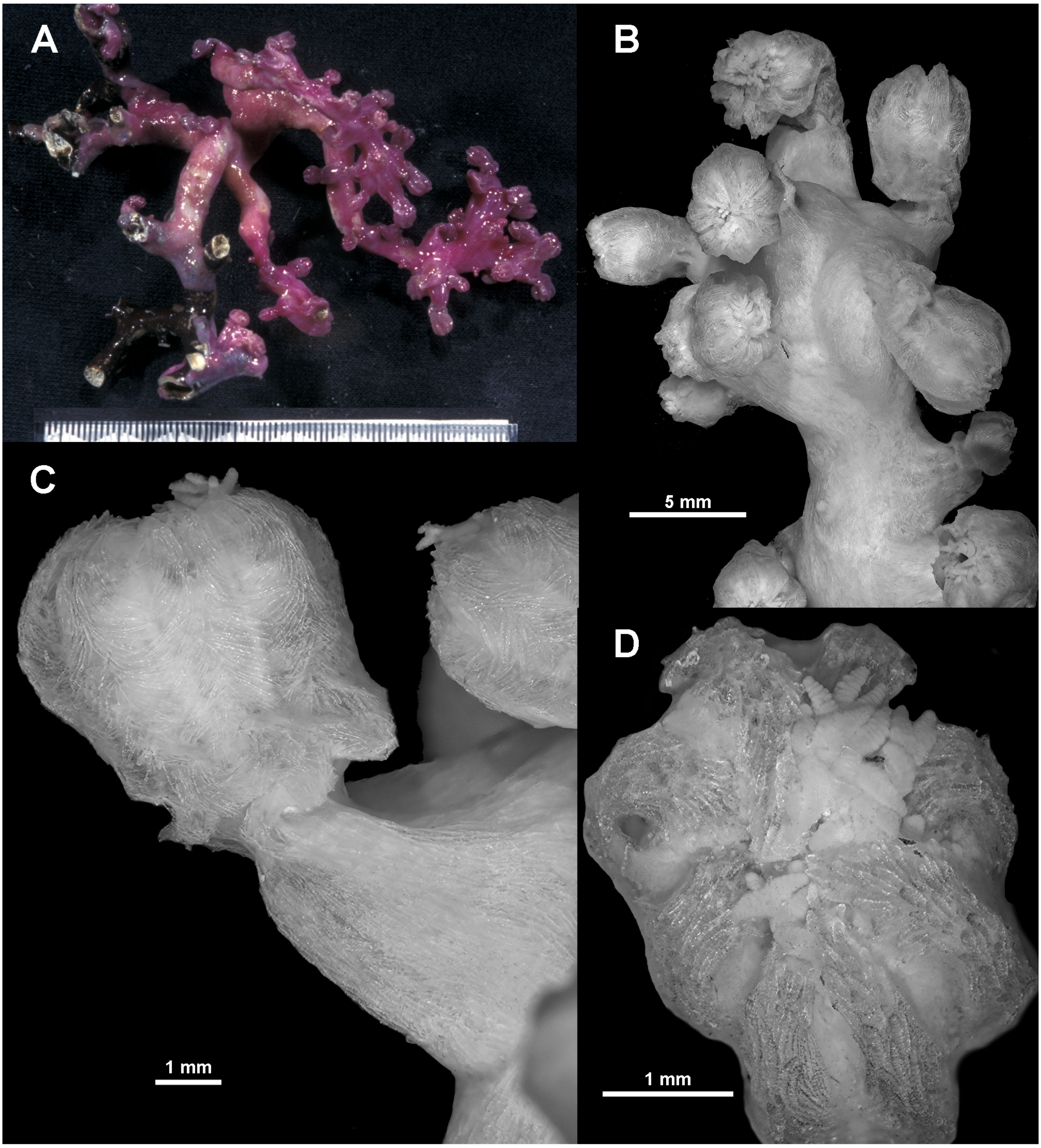

Figure 2.103. *Victorgorgia eminens,* n. sp., NTM CO13050: A. Colony; B. Branch tip with exert polyps; C. Exert polyp; D. Tentacles folded over polyp mouth. (A. courtesy of Karen Gowlett-Holmes, CMAR).

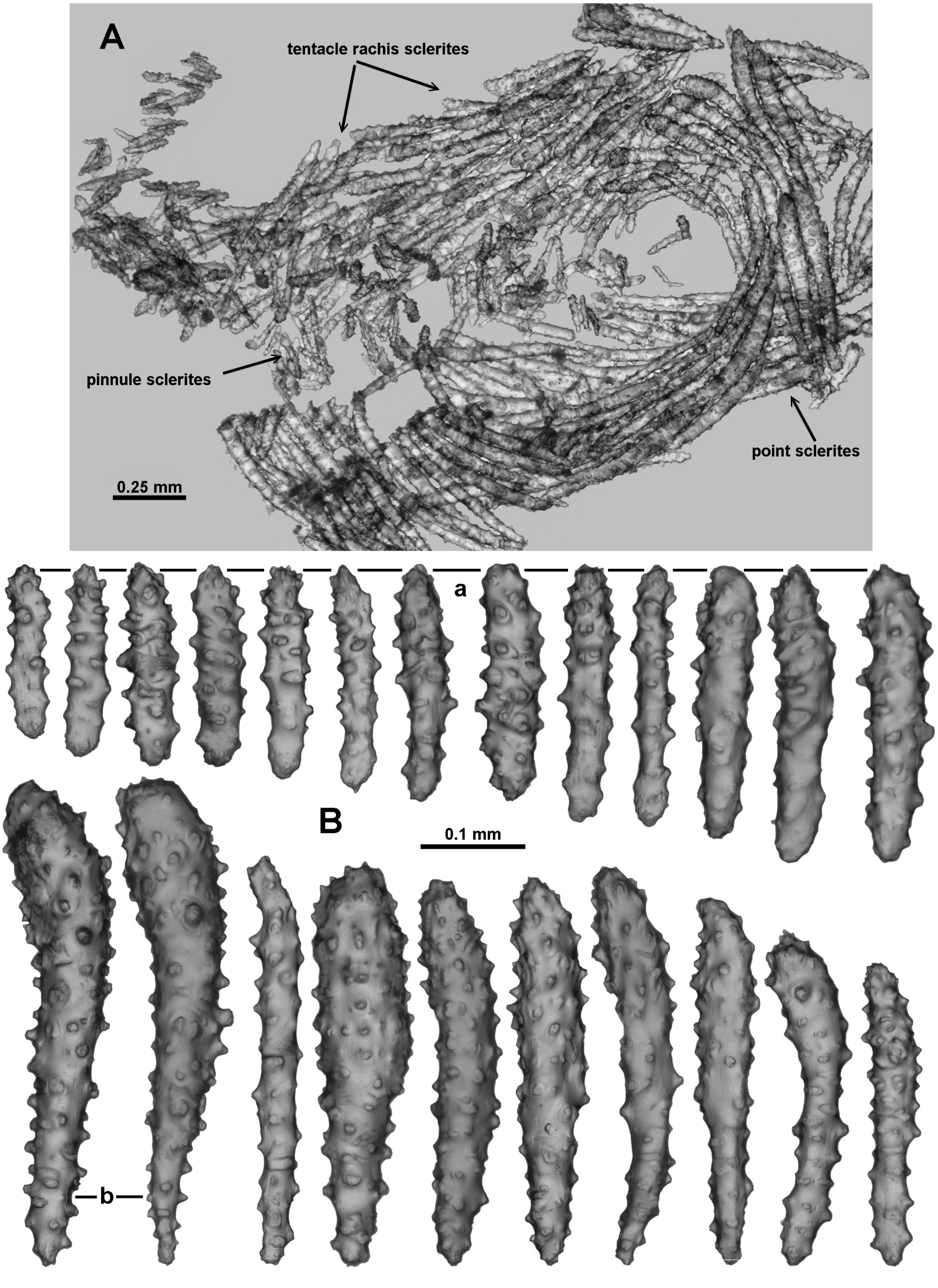

Figure 2.104. *Victorgorgia eminens,* n. sp., NTM CO13050: A. Tentacle and point sclerites in situ; B. Tentacle rachis sclerites (a. tuberculate rods not true josephinae clubs; b. more tuberculate than holotype).

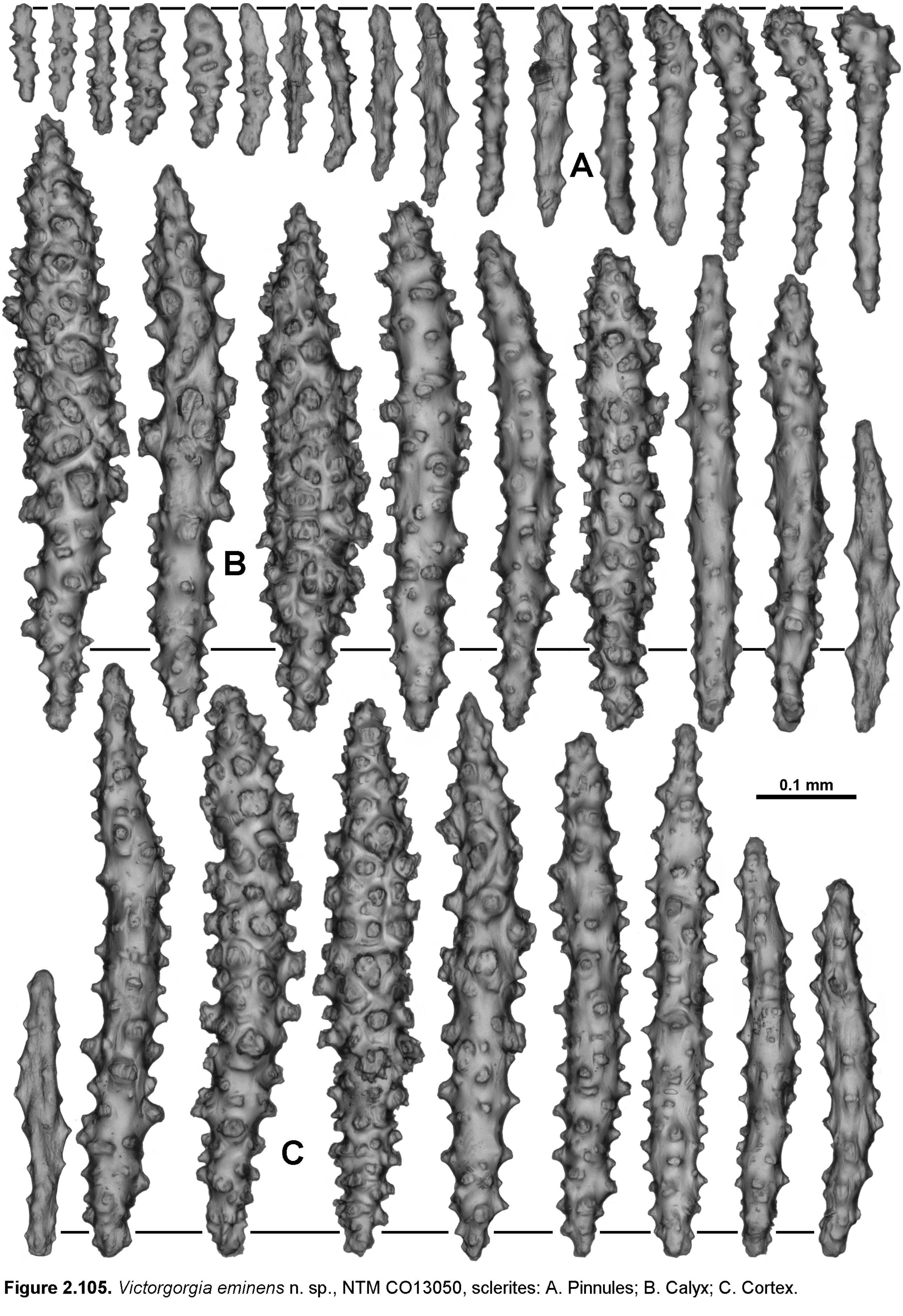

Figure 2.105. *Victorgorgia eminens* n. sp., NTM CO13050, sclerites: A. Pinnules; B. Calyx; C. Cortex.

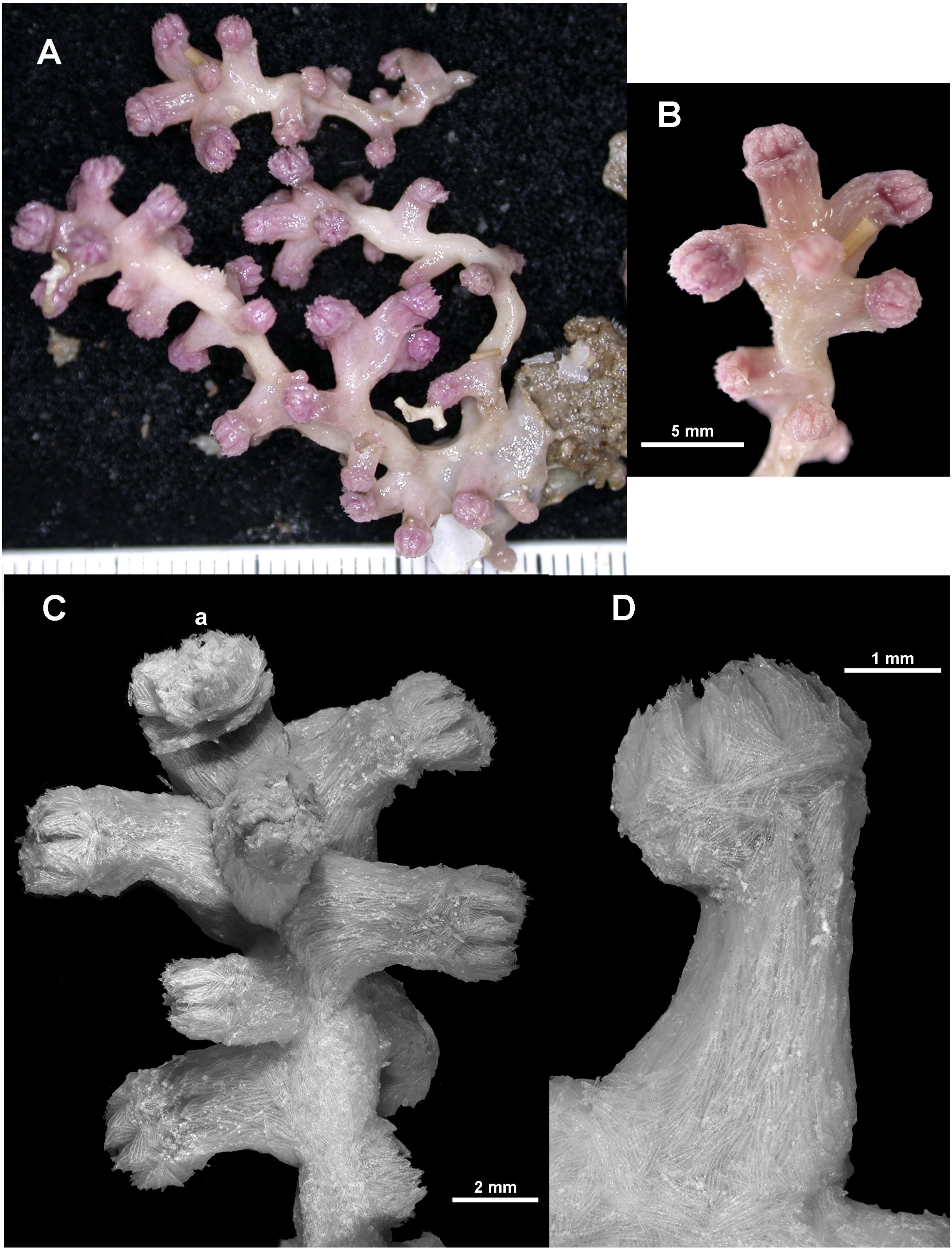

Figure 2.106. *Victorgorgia nyahae* n. sp., holotype: A. Colony; B-C. Branch tip (Ca. flattened polyp head); D. Polyp. (A-B. Courtesy of Karen Gowlett-Holmes, CMAR).

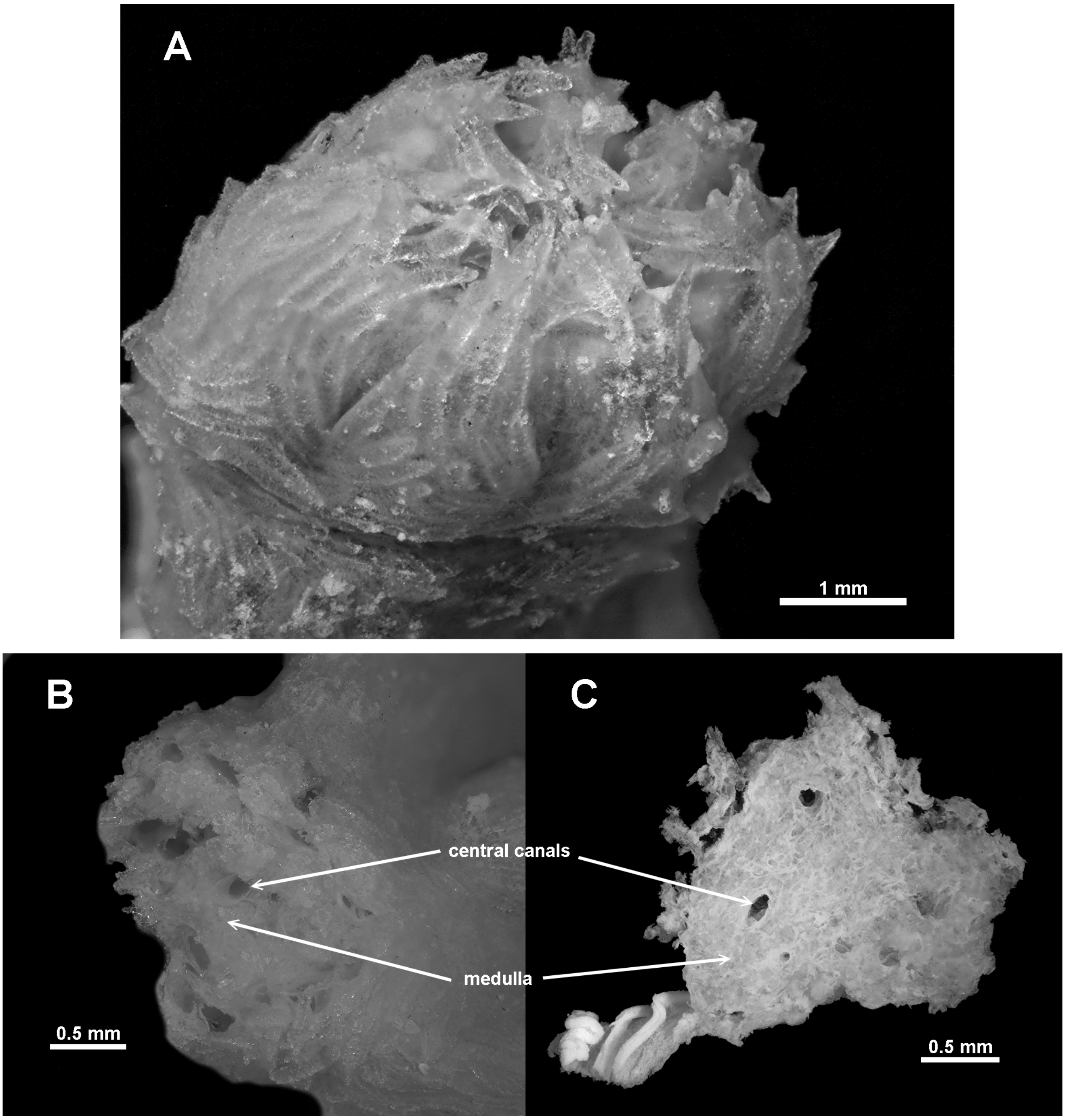

Figure 2.107. *Victorgorgia nyahae* n. sp., holotype: A. Polyp head; B. Cross-section of medulla; C. Decalcified cross-section of medulla.

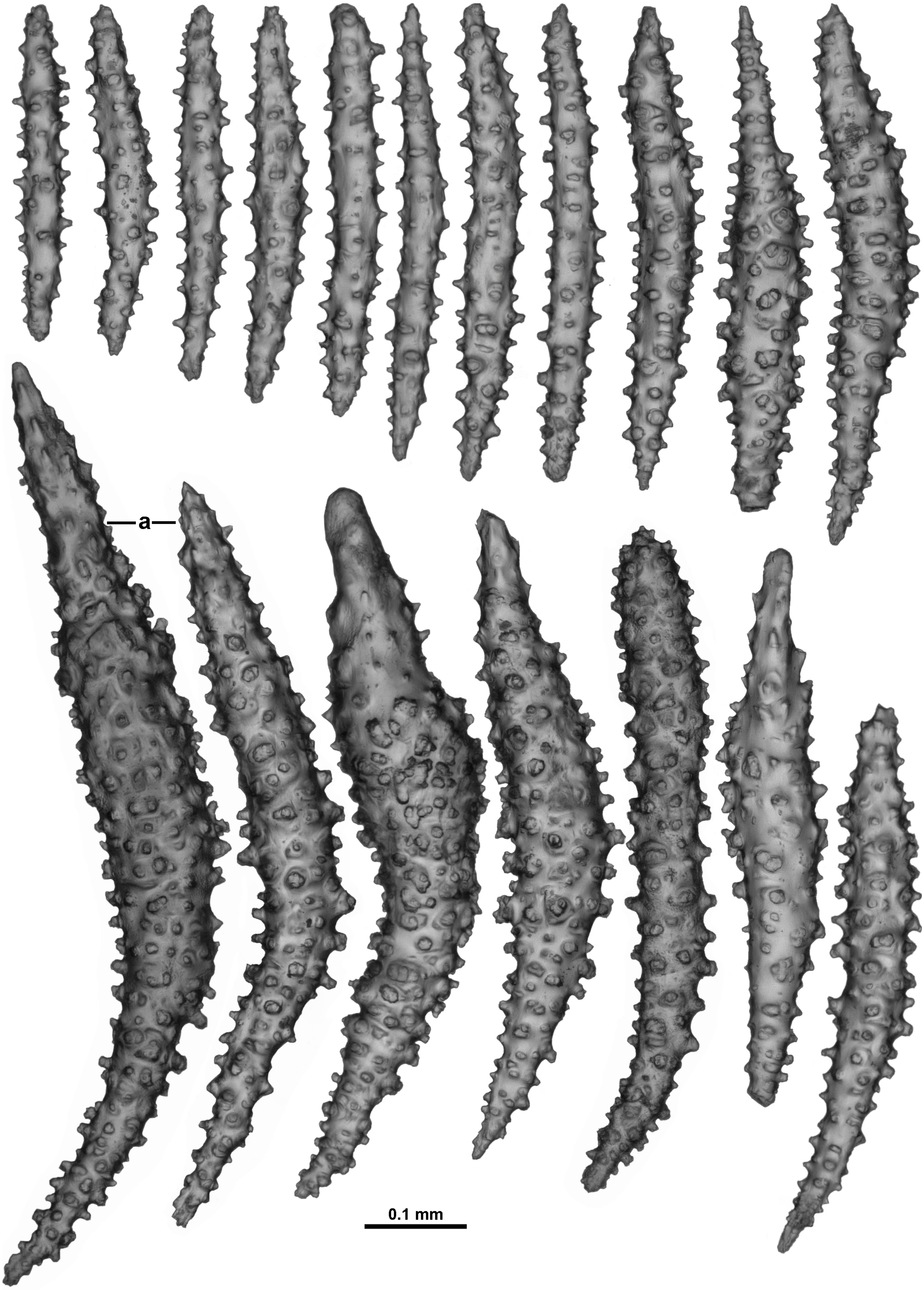

Figure 2.108. *Victorgorgia nyahae* n. sp., holotype, sclerites: Point (a. spear tips).

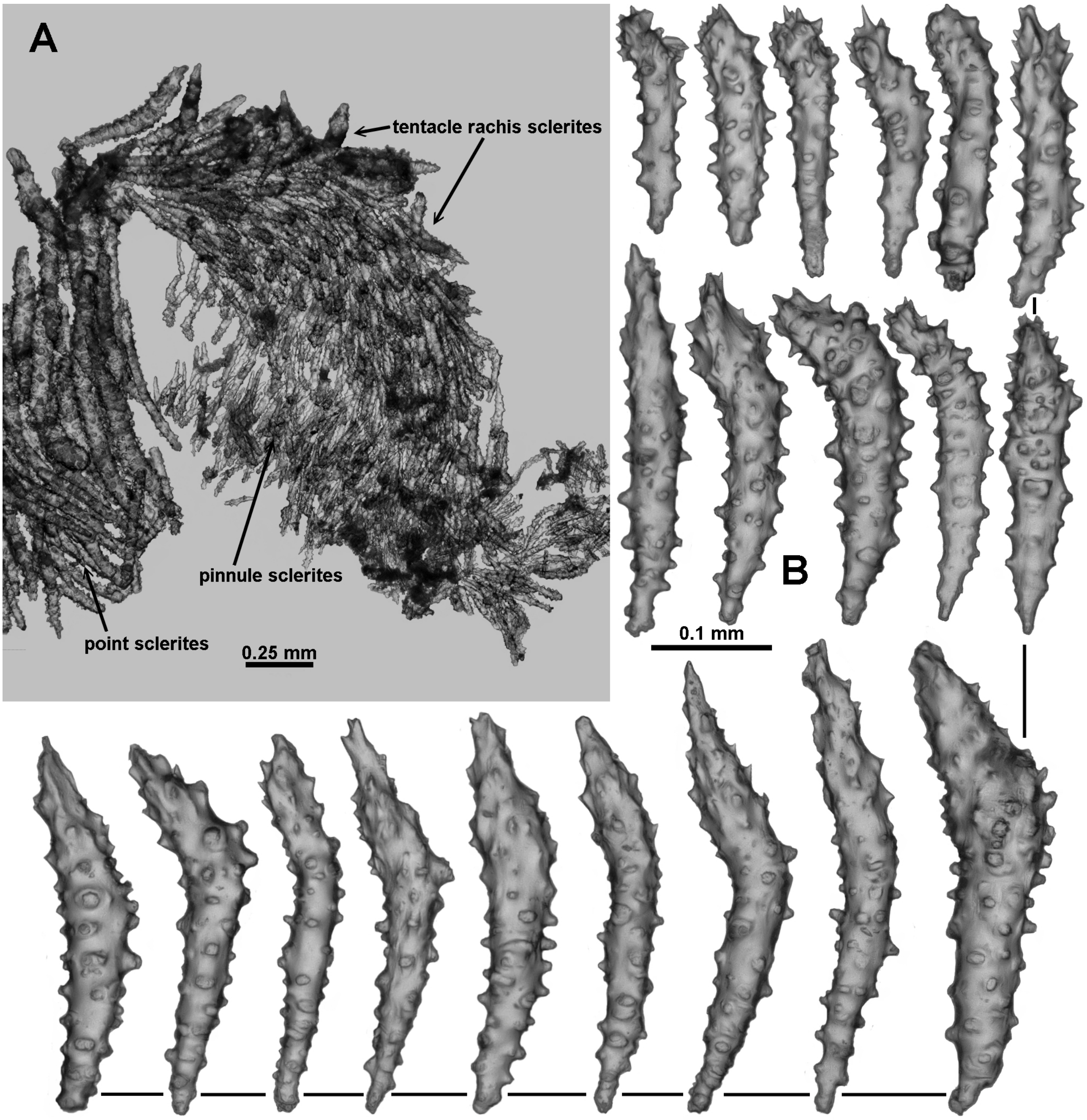

Figure 2.109. *Victorgorgia nyahae* n. sp., holotype: A. Tentacle and point sclerites in situ; B. Tentacle rachis sclerites.

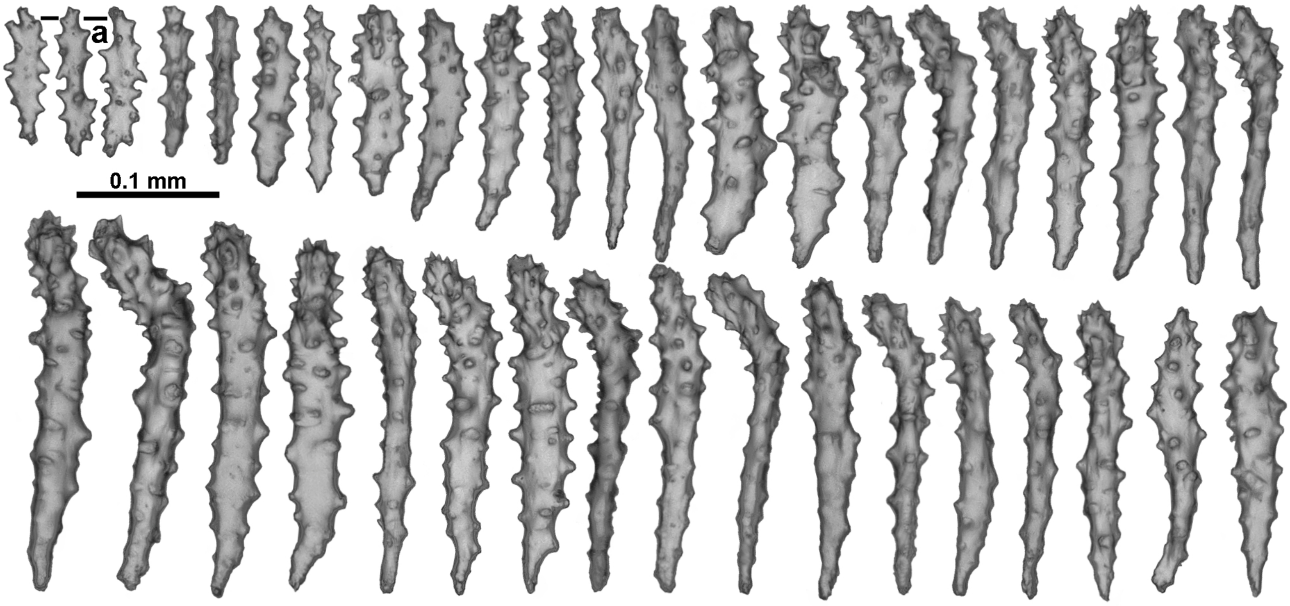

Figure 2.110. *Victorgorgia nyahae* n. sp., holotype, sclerites: Pinnule (a. flat rods with jagged edges).

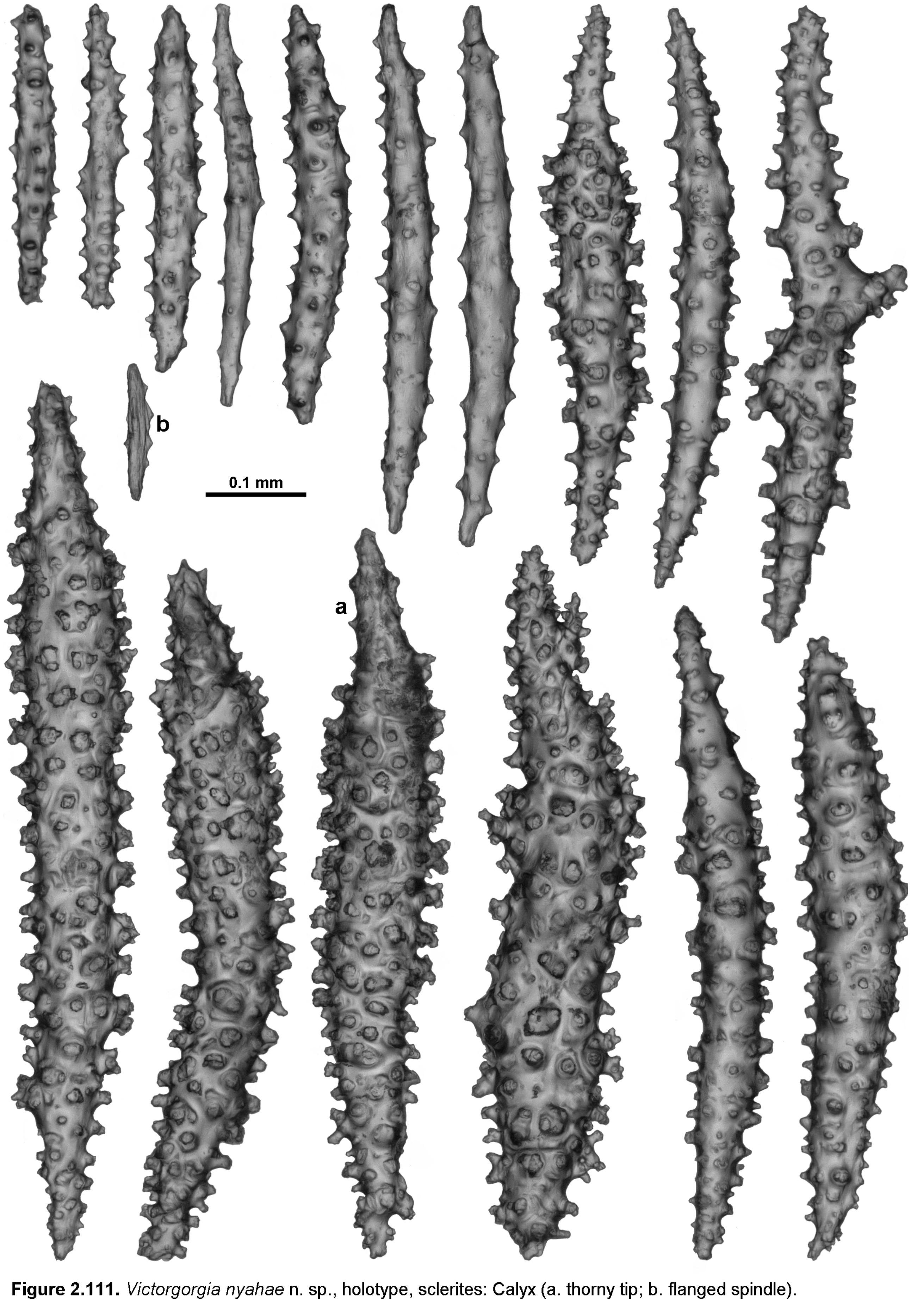

Figure 2.111. *Victorgorgia nyahae* n. sp., holotype, sclerites: Calyx (a. thorny tip; b. flanged spindle).

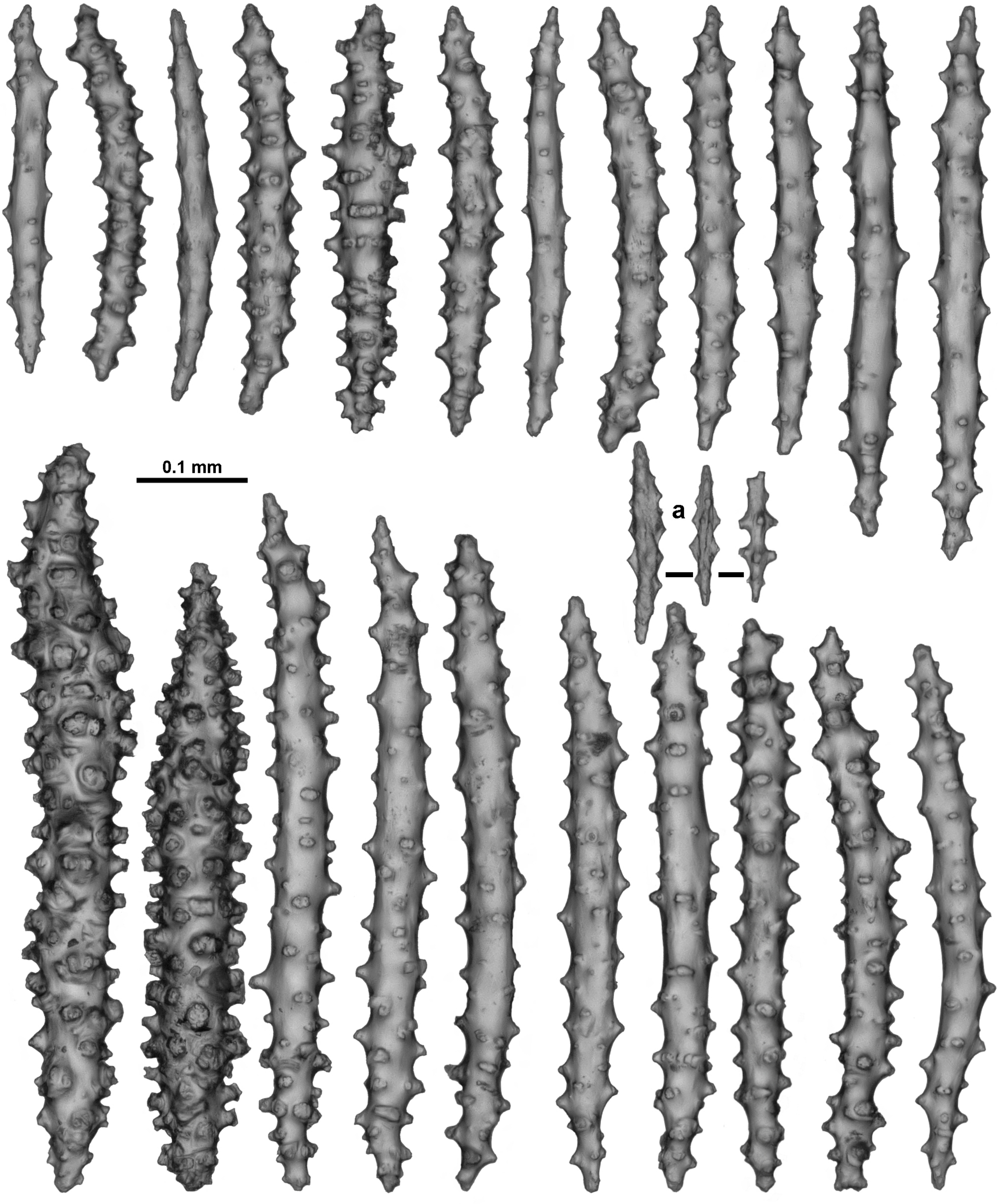

Figure 2.112. *Victorgorgia nyahae* n. sp., holotype, sclerites: Cortex (a. flanged spindles).

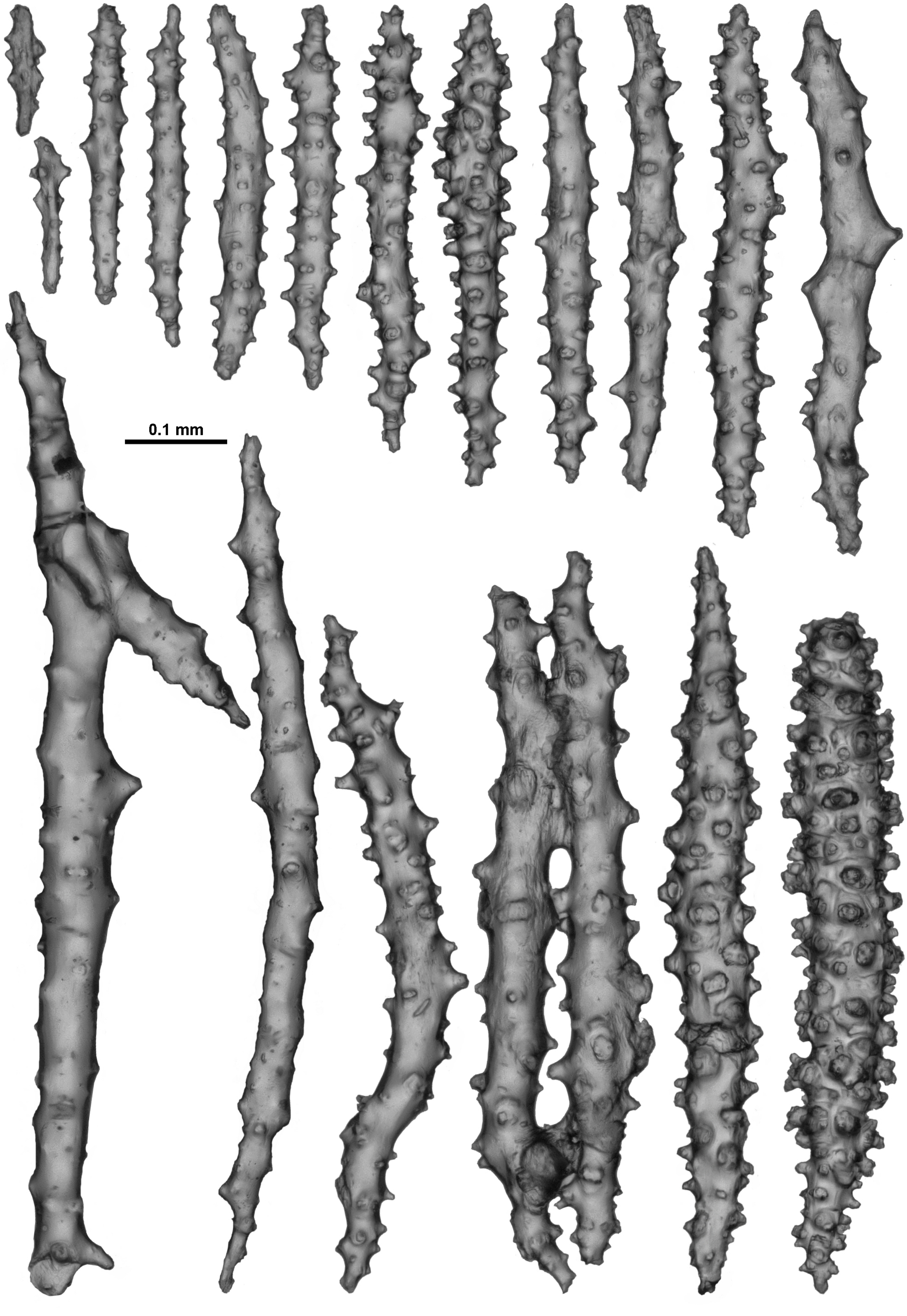

Figure 2.113. *Victorgorgia nyahae* n. sp., holotype, sclerites: Medulla.

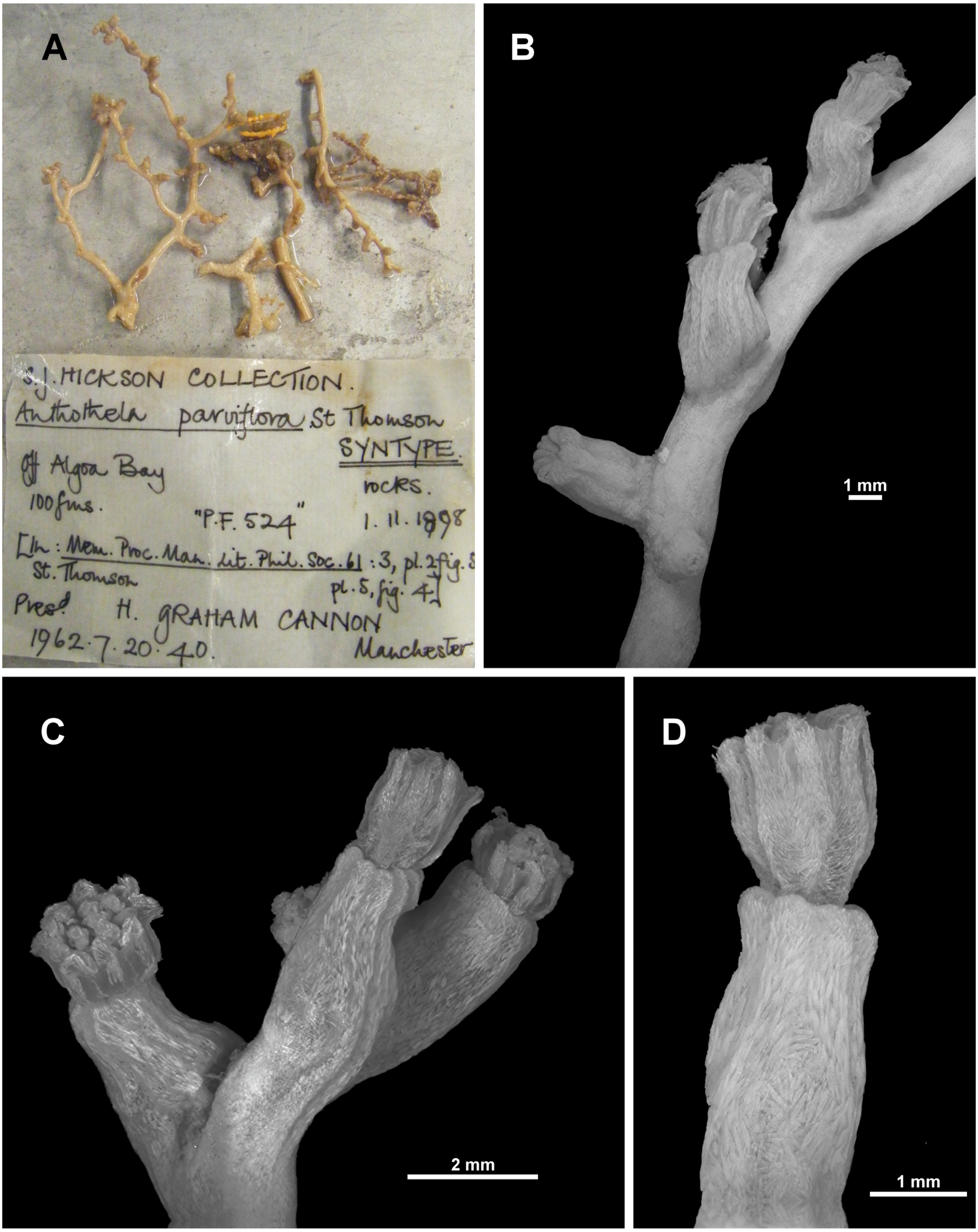

Figure 2.114. *Williamsius parviflora,* (Thomson, 1916), paralectotype: A. Paralectoype lot; B. Branch fragment; C. Branch tip; D. Polyp. (A. Courtesy of NHMUK staff).

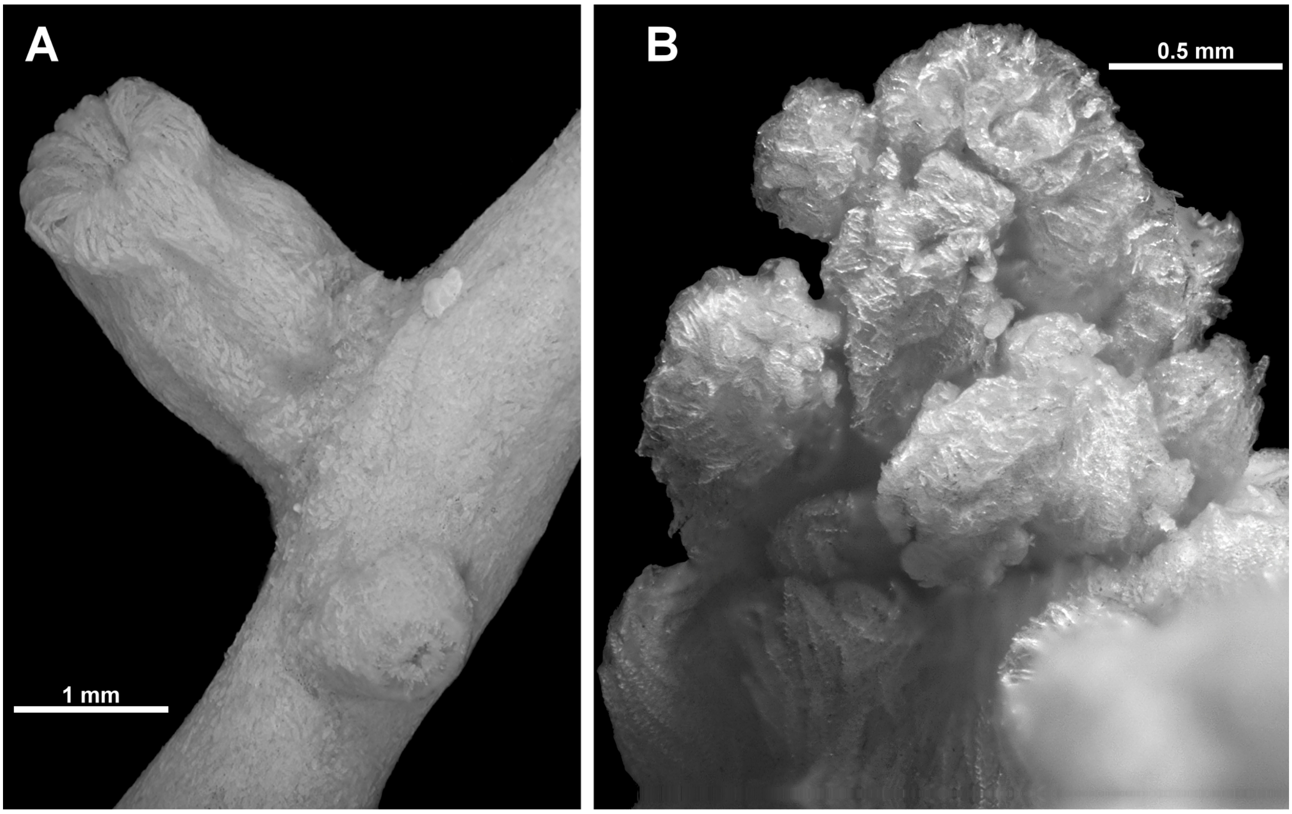

Figure 2.115. *Williamsius parviflora,* (Thomson, 1916), paralectotype: A. Retracted polyp; B. Crumpled tentacles.

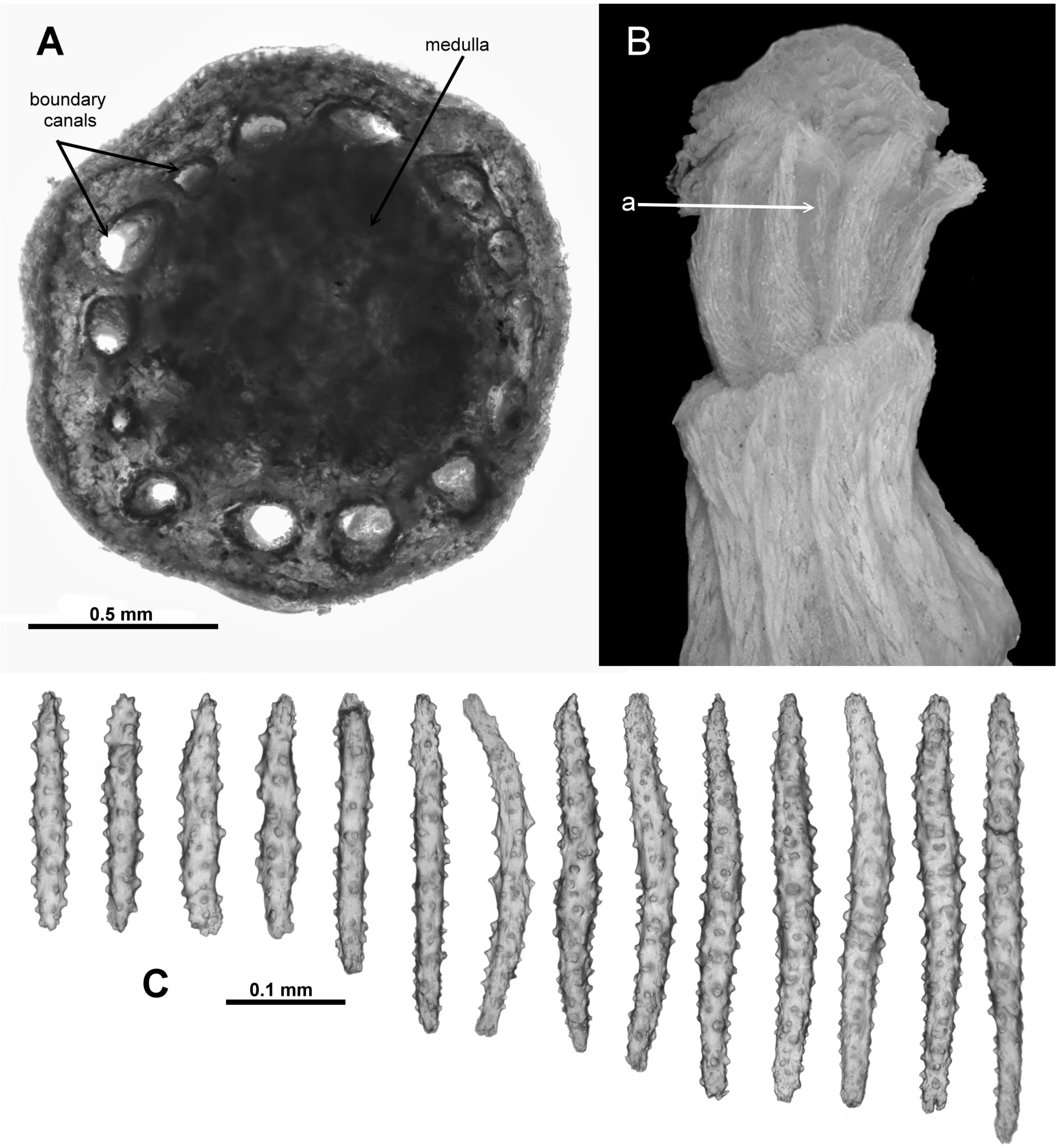

Figure 2.116. *Williamsius parviflora,* (Thomson, 1916), paralectotype: A. Decalcified cross-section of medulla; B. Polyp head (a. intermediate sclerites); C. Point sclerites.

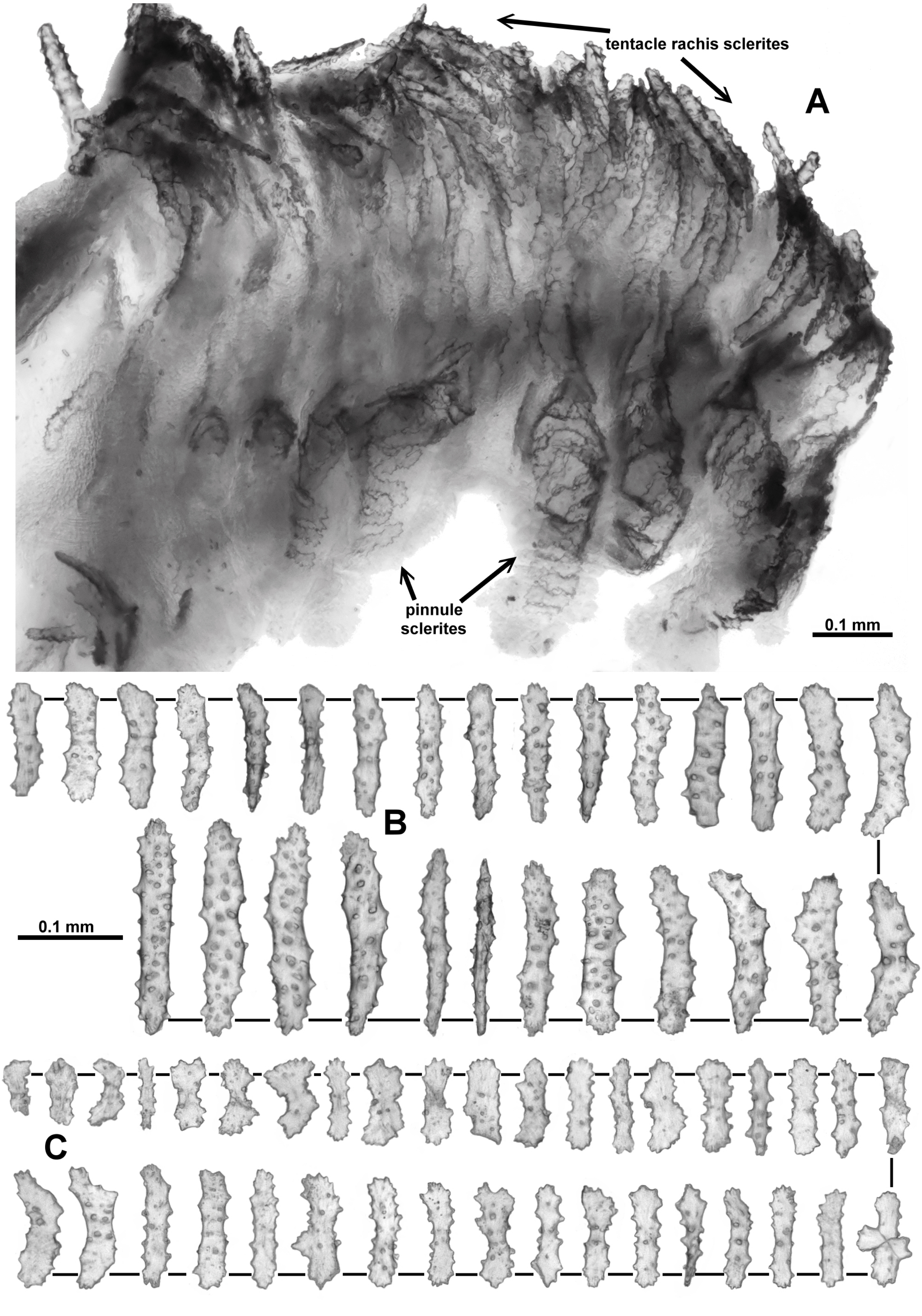

Figure 2.117. *Williamsius parviflora,* (Thomson, 1916), paralectotype: A. Tentacle with sclerites in situ; B. Tentacular rachis sclerites; C. Pinnule sclerites.

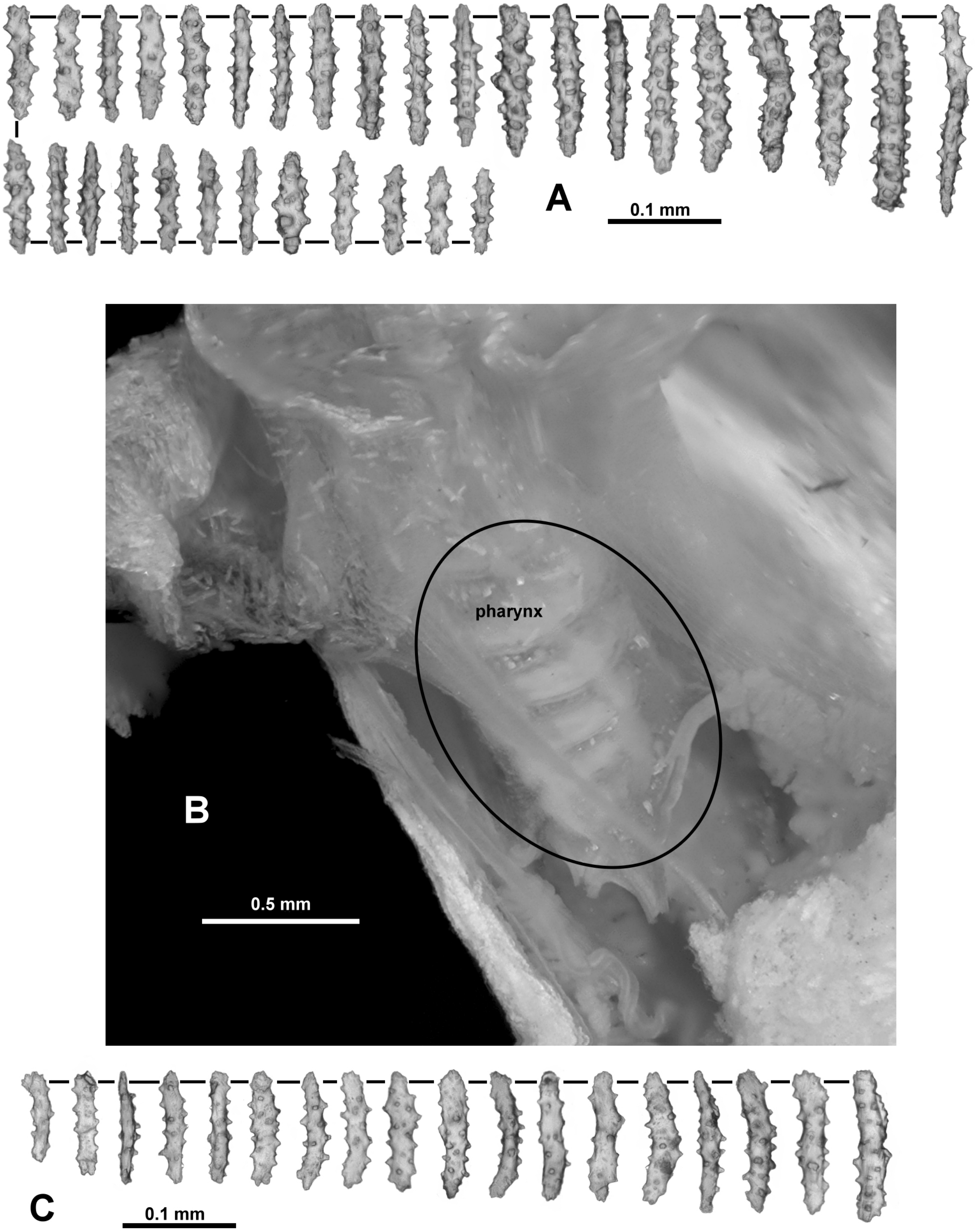

Figure 2.118. *Williamsius parviflora,* (Thomson, 1916), paralectotype: A. Neck sclerites; B. Pharynx in place; C. Pharynx sclerites.

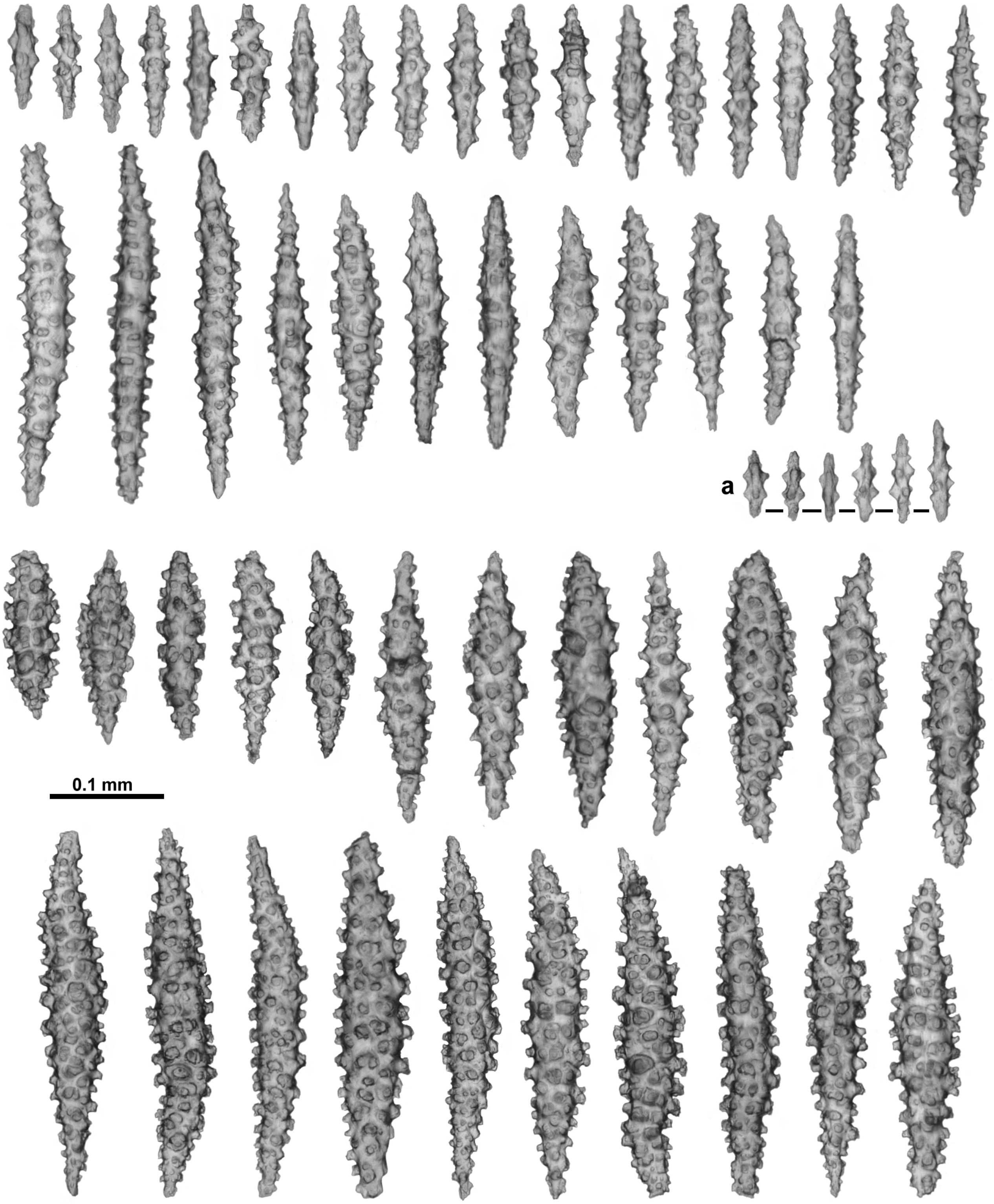

Figure 2.119. *Williamsius parviflora,* (Thomson, 1916), paralectotype, sclerites: Calyx (a. flanged sclerites).

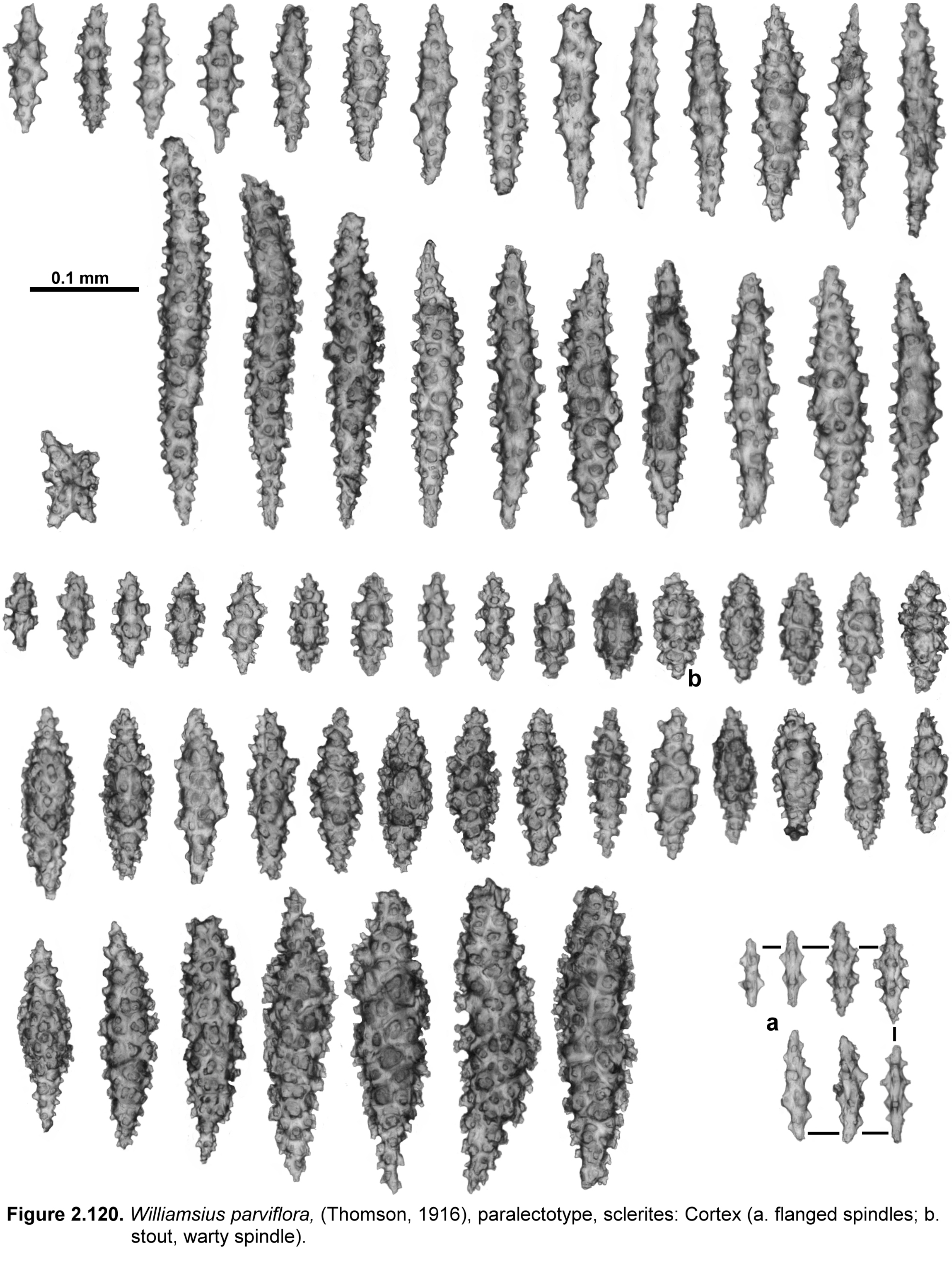

Figure 2.120. *Williamsius parviflora,* (Thomson, 1916), paralectotype, sclerites: Cortex (a. flanged spindles; b. stout, warty spindle).

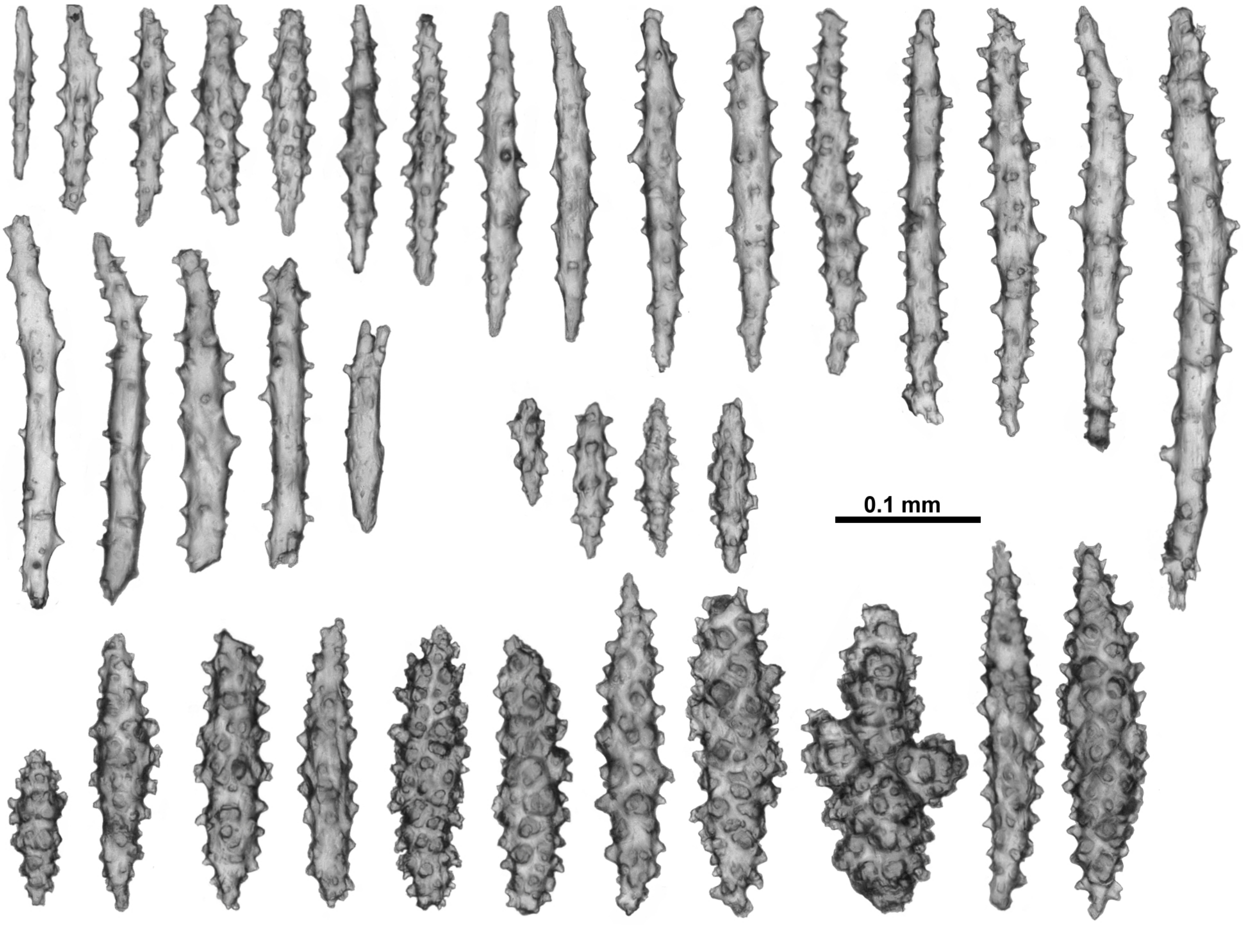

Figure 2.121. *Williamsius parviflora,* (Thomson, 1916), paralectotype, sclerites: Medulla.

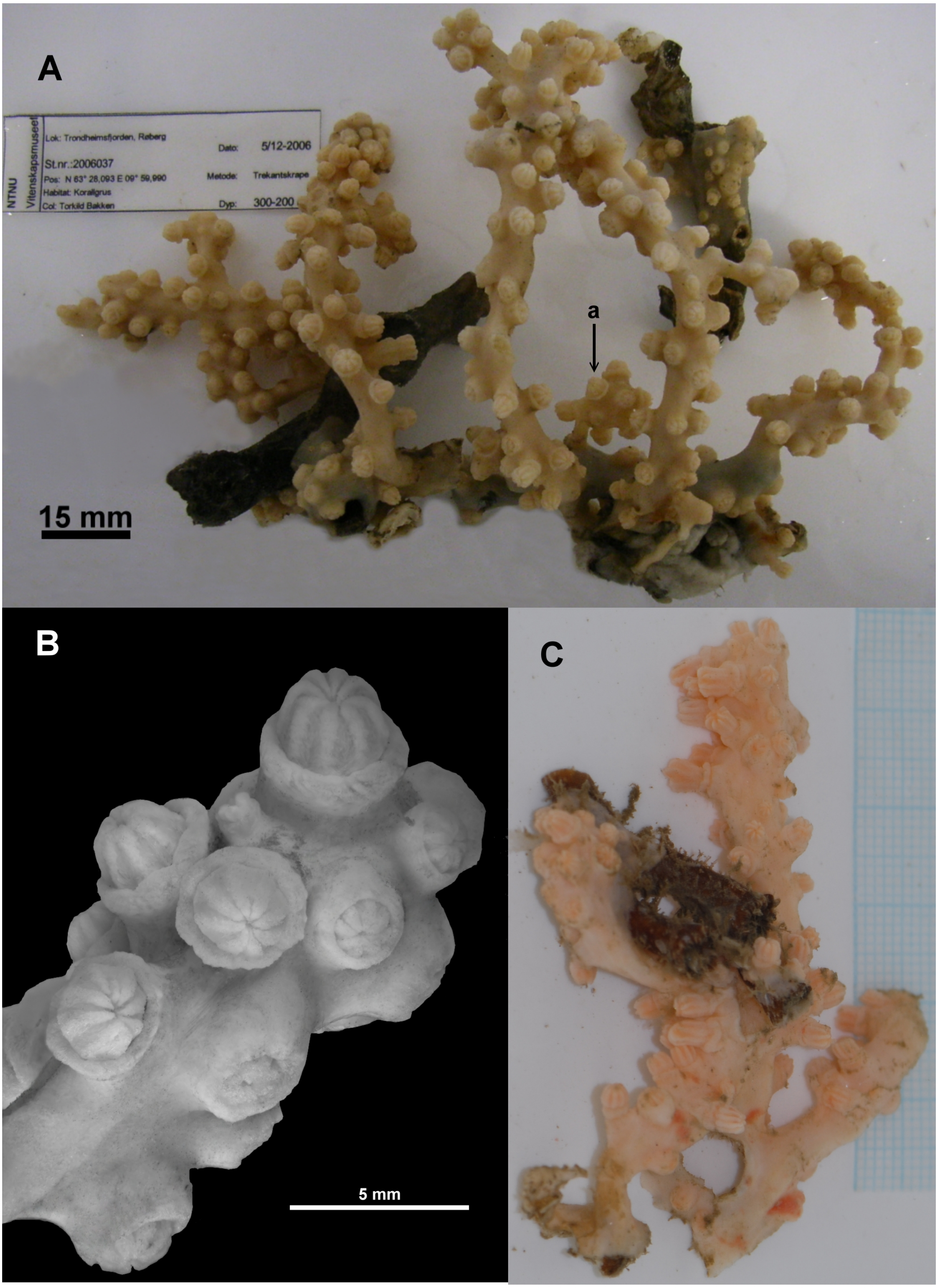

Figure 2.122. *Lateothela anitorkilda,* n.gen., n. sp.: A-B. Holotype: (A). Colony (a. short side branch); (B). Branch tip. C. Paratype NTNU 67147, recently collected colony. (C. Courtesy of Torkild Bakken, NTNU).

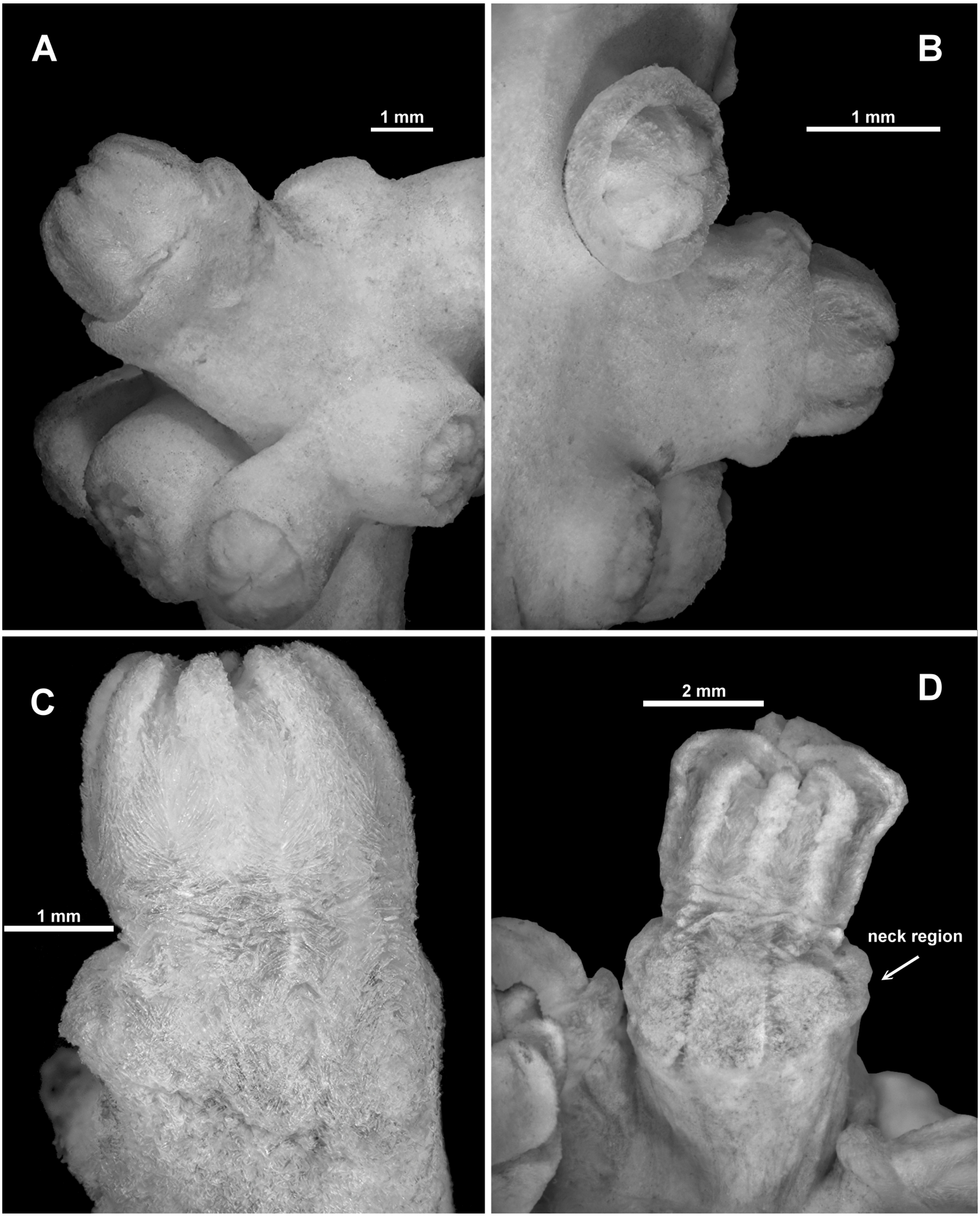

Figure 2.123. *Lateothela anitorkilda,* n. gen., n. sp., holotype: A. Polyp bunch; B. Partly retracted polyps; C. Extended polyp; D. Polyp neck.

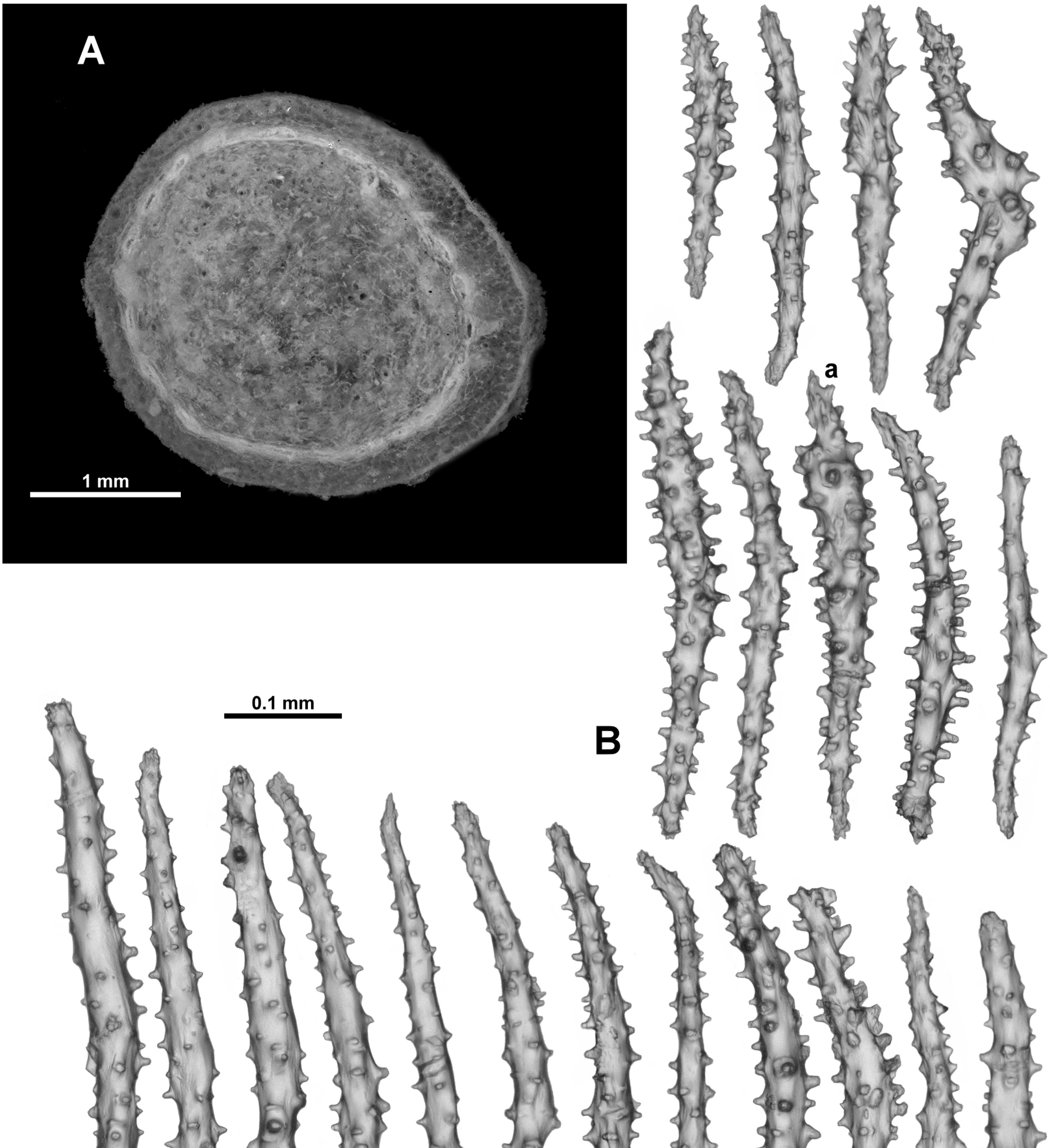

Figure 2.124. *Lateothela anitorkilda,* n. gen., n. sp., holotype: A. Decalcified cross-section of medulla; B. Point sclerites (a. slightly more clavate sclerite).

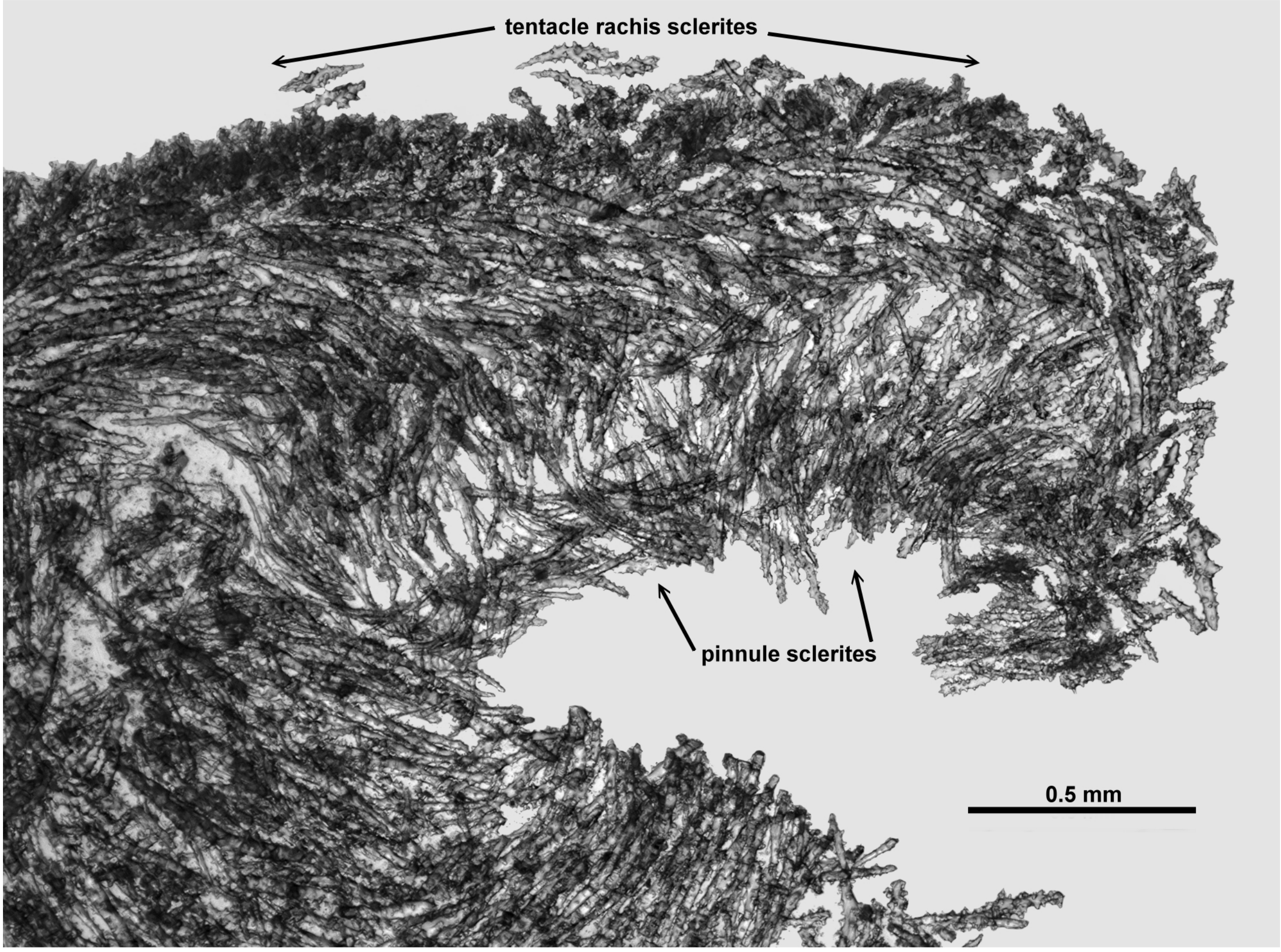

Figure 2.125. *Lateothela anitorkilda,* n. gen.,n, sp., holotype: Tentacle with sclerites in situ.

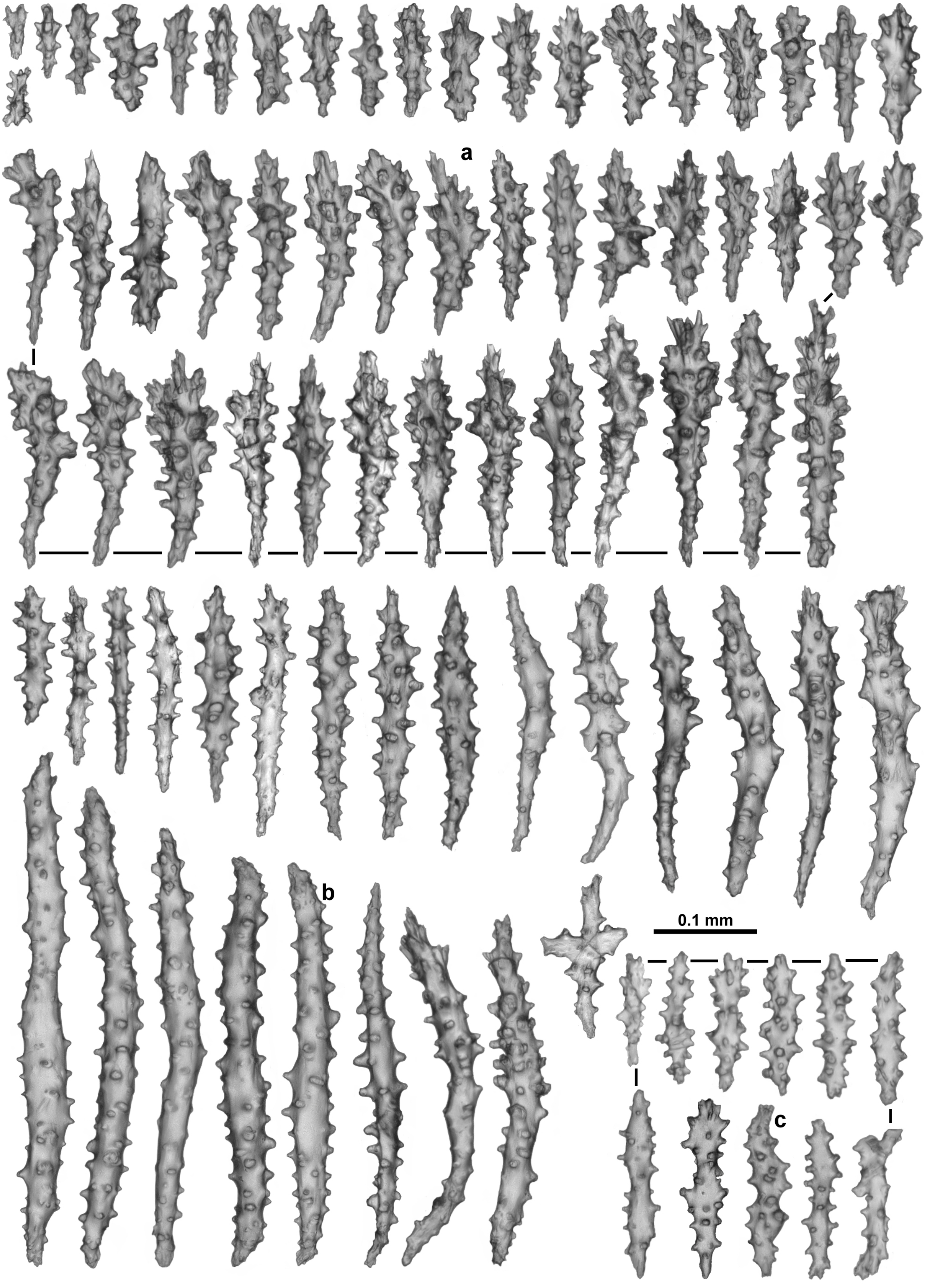

Figure 2.126. *Lateothela anitorkilda,* n. gen., n. sp., holotype, sclerites: Tentacle rachis (a. clubs with flame-like spikes; b. straight spiny-spindle; c. flat rods).

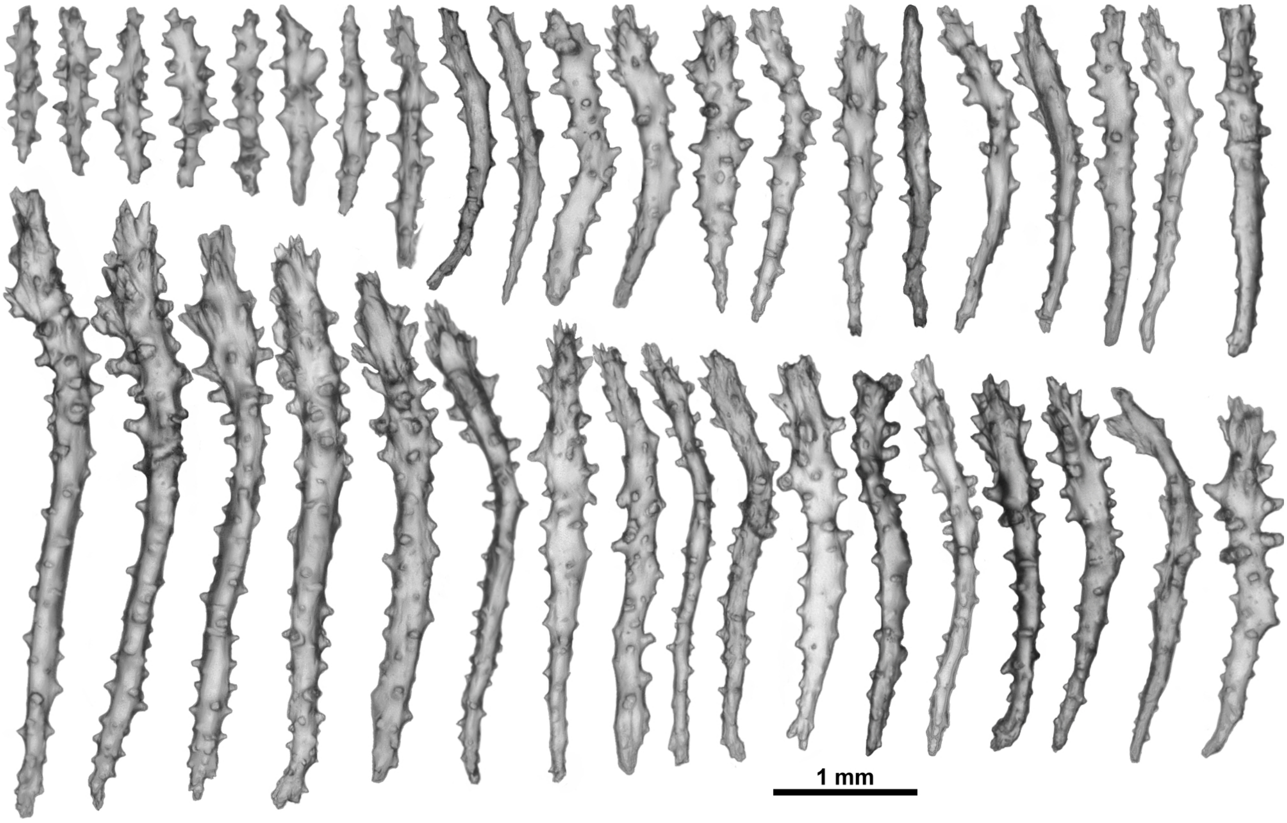

Figure 2.127. *Lateothela anitorkilda,* n. gen, n. sp., holotype, sclerites: Pinnules.

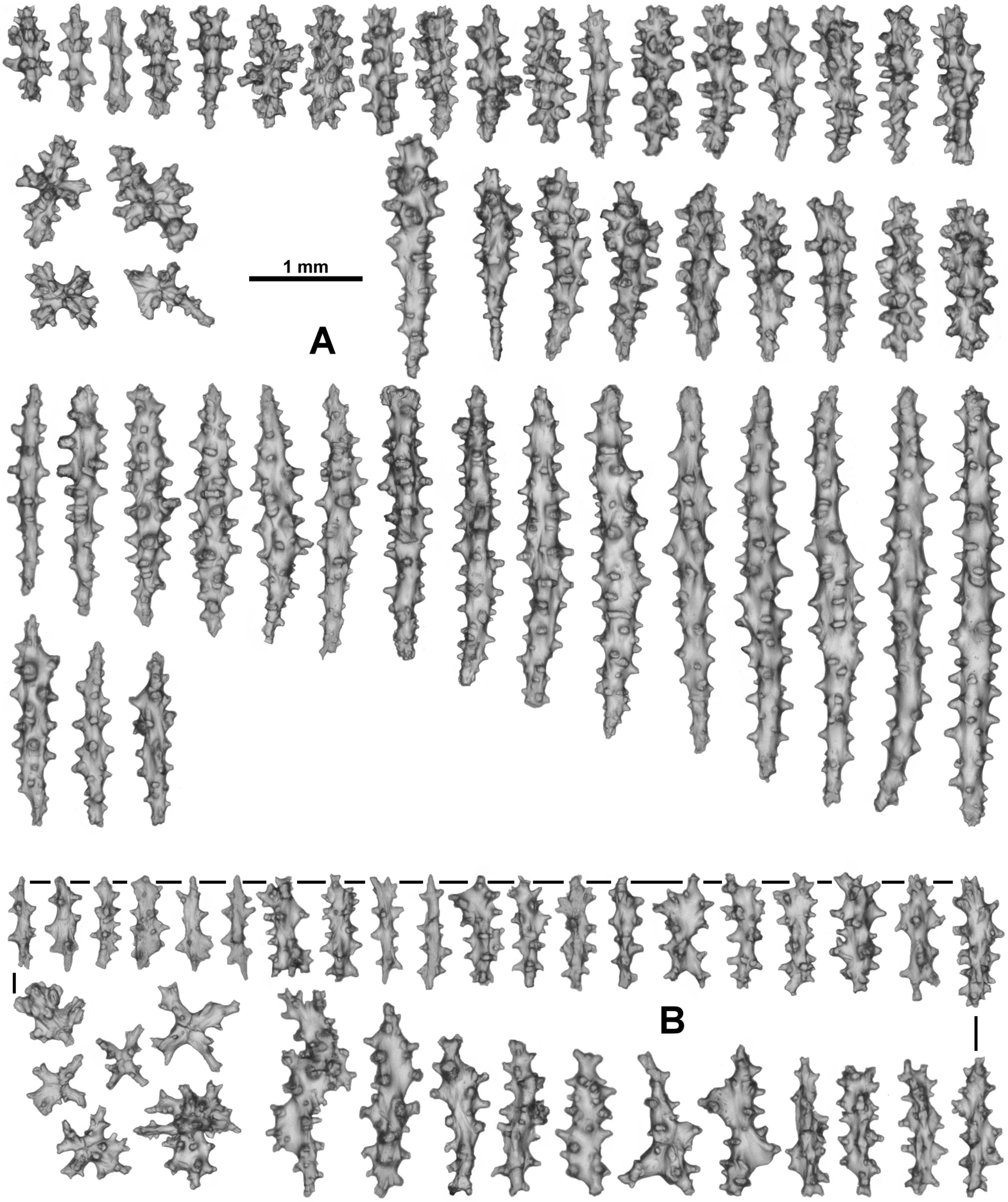

Figure 2.128. *Lateothela anitorkilda,* n. gen., n. sp., holotype, sclerites: A. Neck; B. Pharynx.

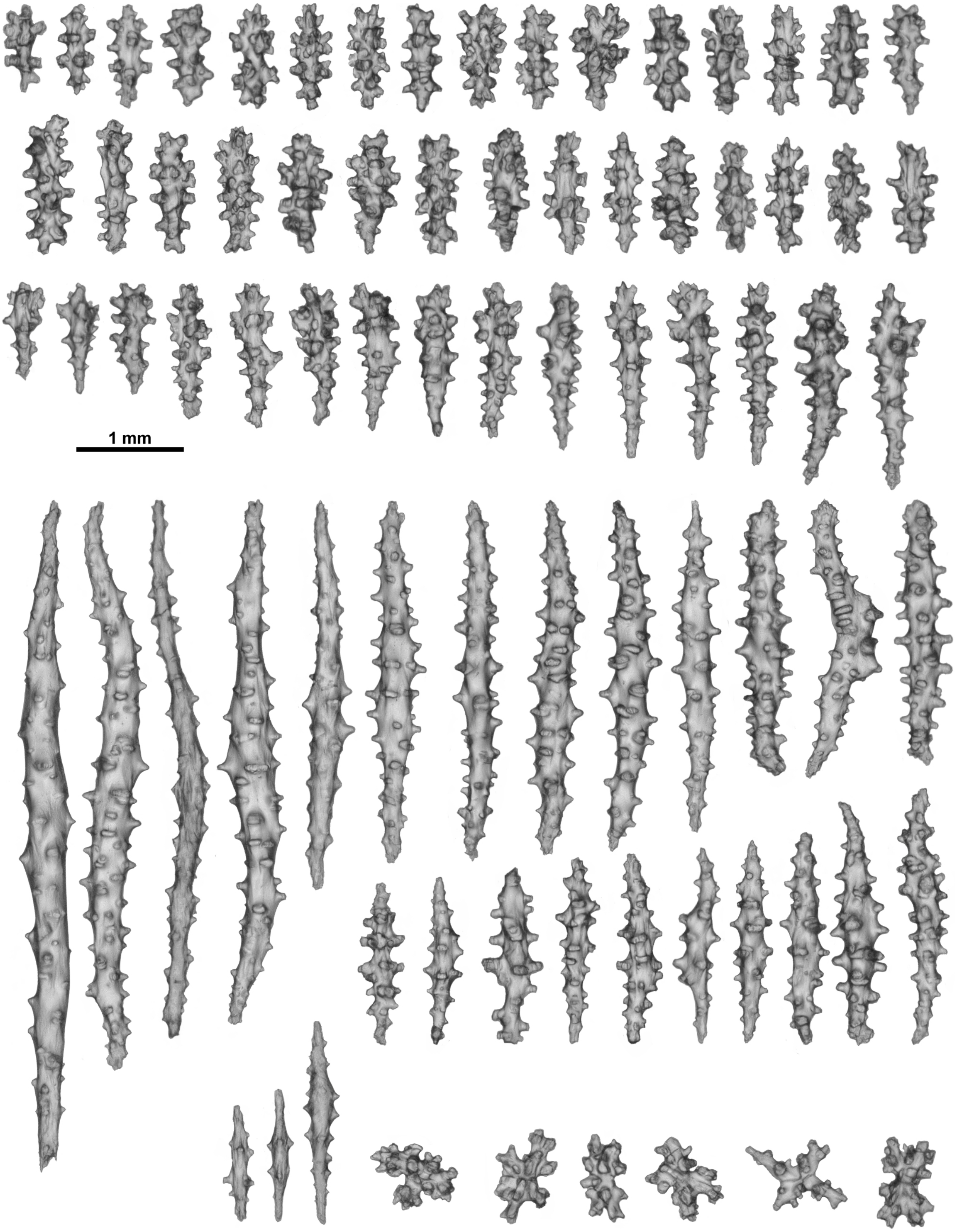

Figure 2.129. *Lateothela anitorkilda,* n. gen., n. sp., holotype, sclerites: Calyx.

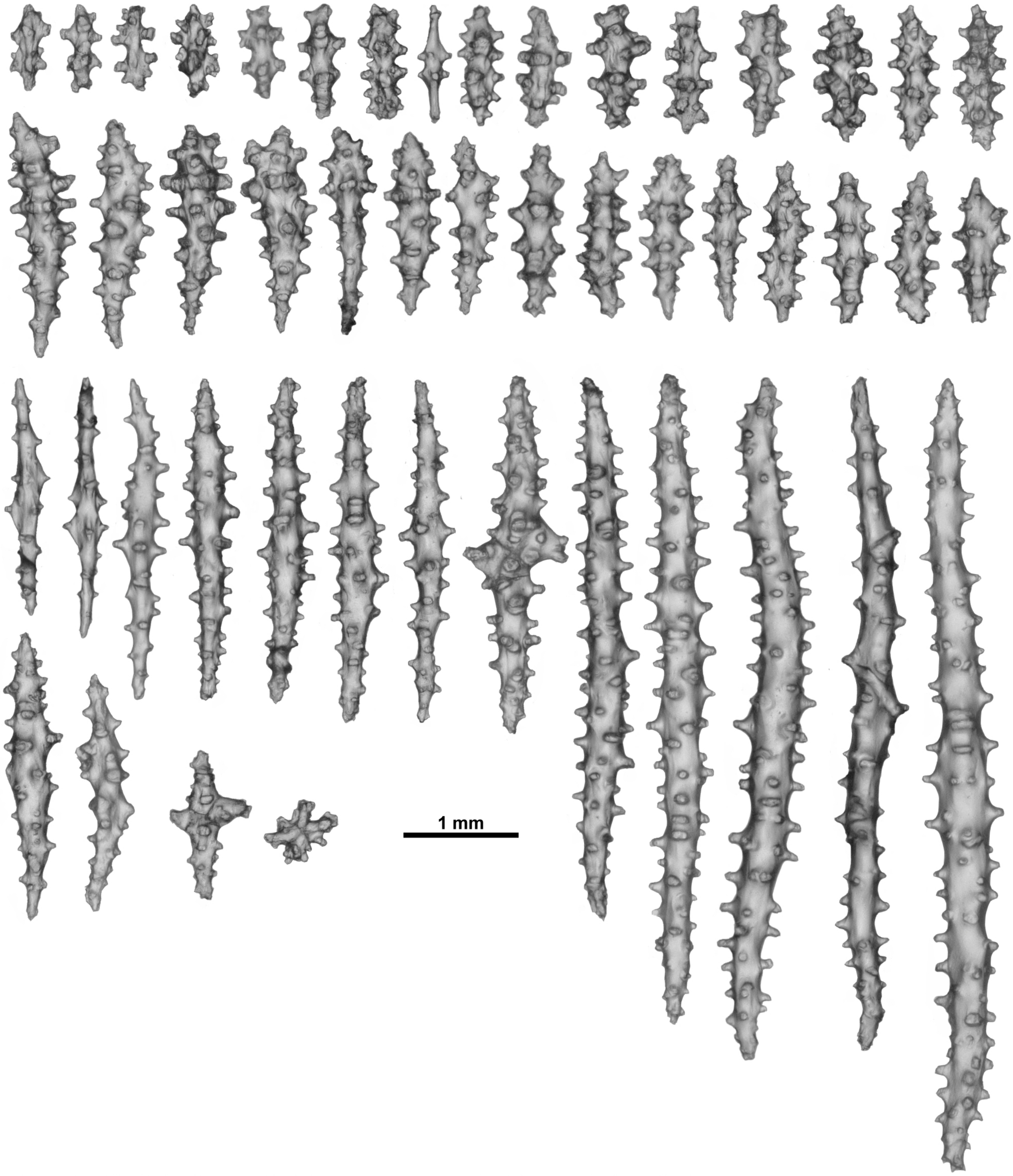

Figure 2.130. *Lateothela anitorkilda,* n. gen., n. sp., holotype, sclerites: Cortex.

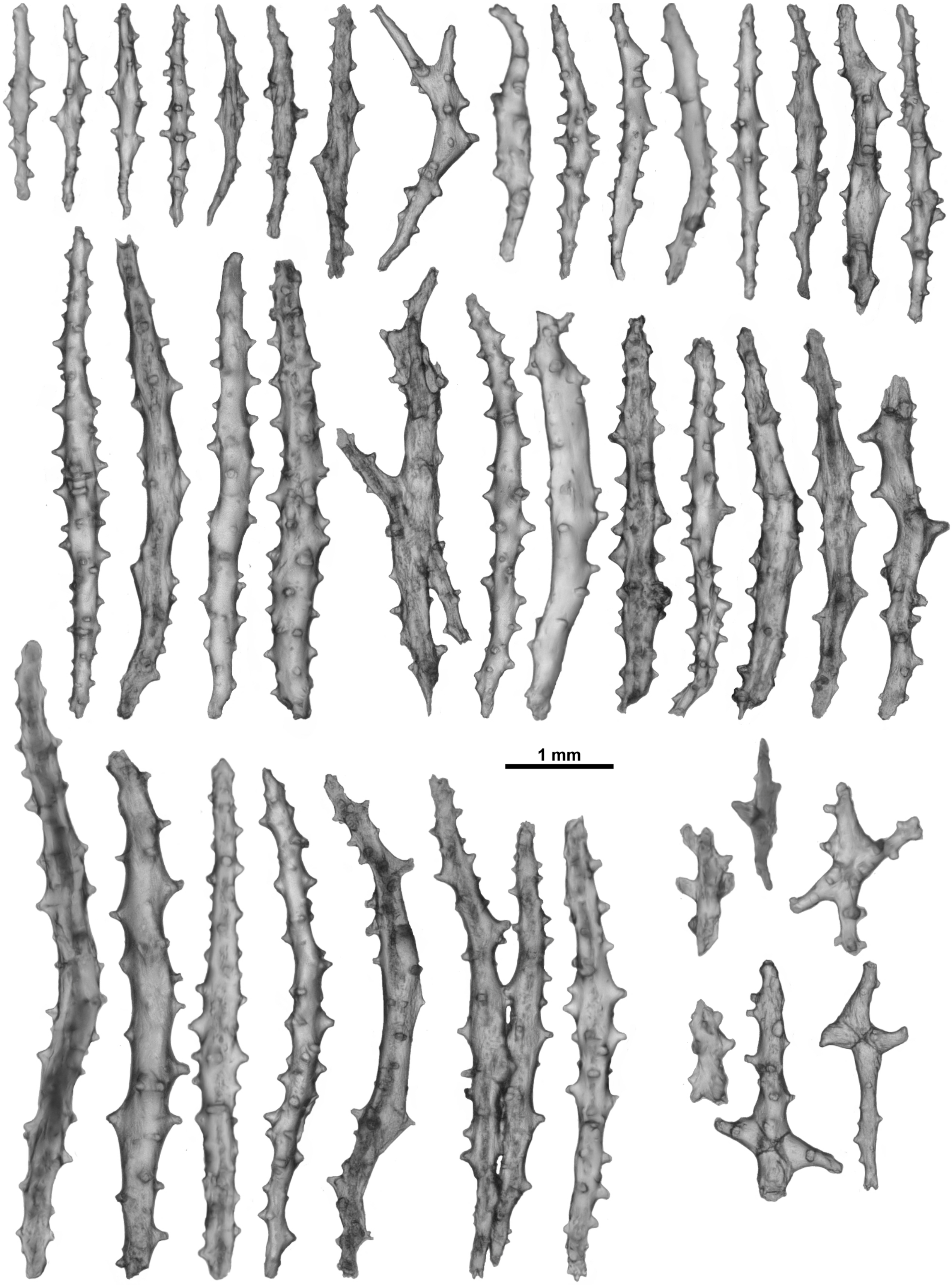

Figure 2.131. *Lateothela anitorkilda,* n. gen., n. sp., holotype, sclerites: Medulla.

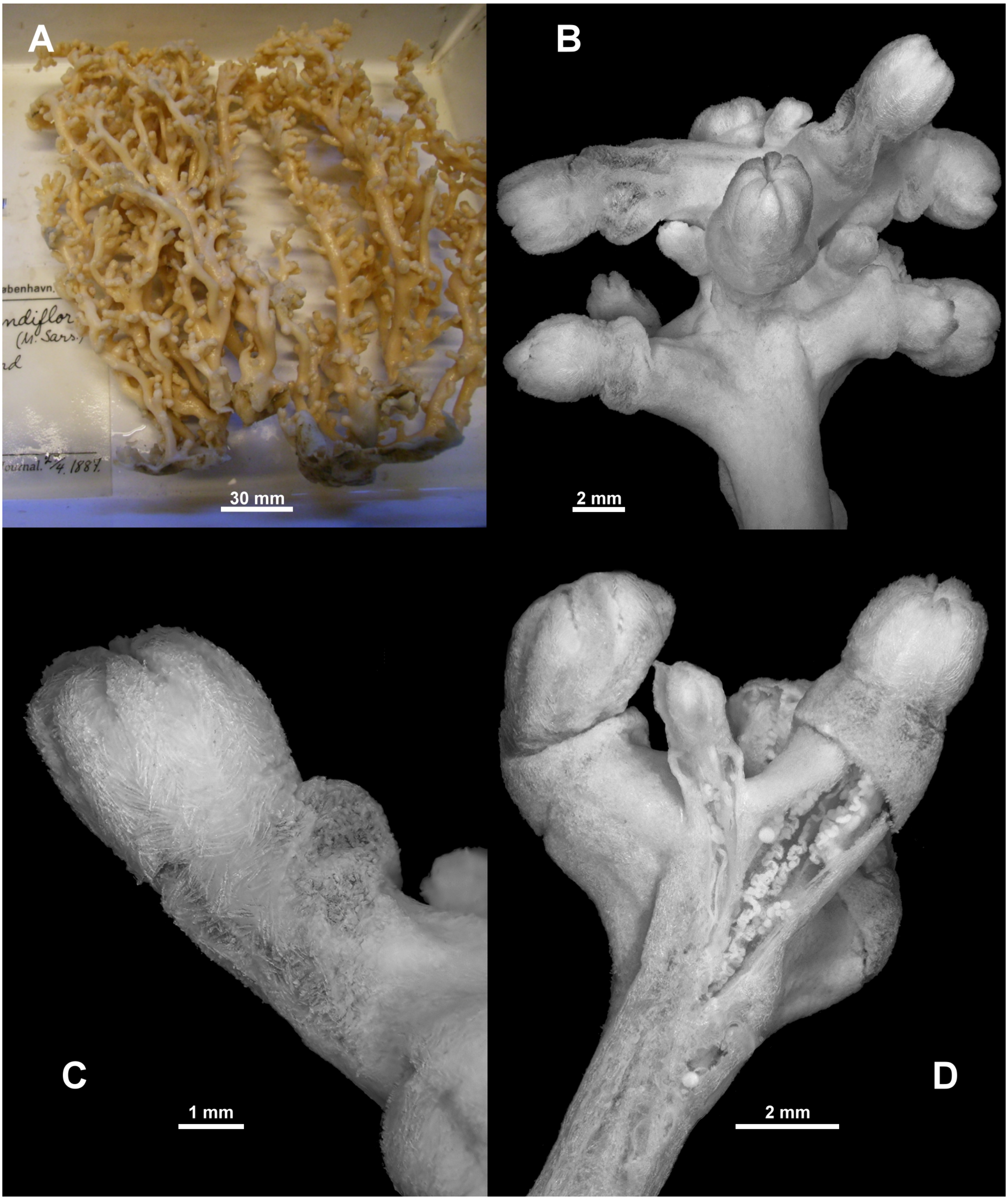

Figure 2.132. *Lateothela anitorkilda,* n. gen., n. sp., paratype, ZMUC-ANT-000468 : A. Colony; B. Polyp bunch; C. Extended polyp; D. Longitudinal section of polyp bunch.

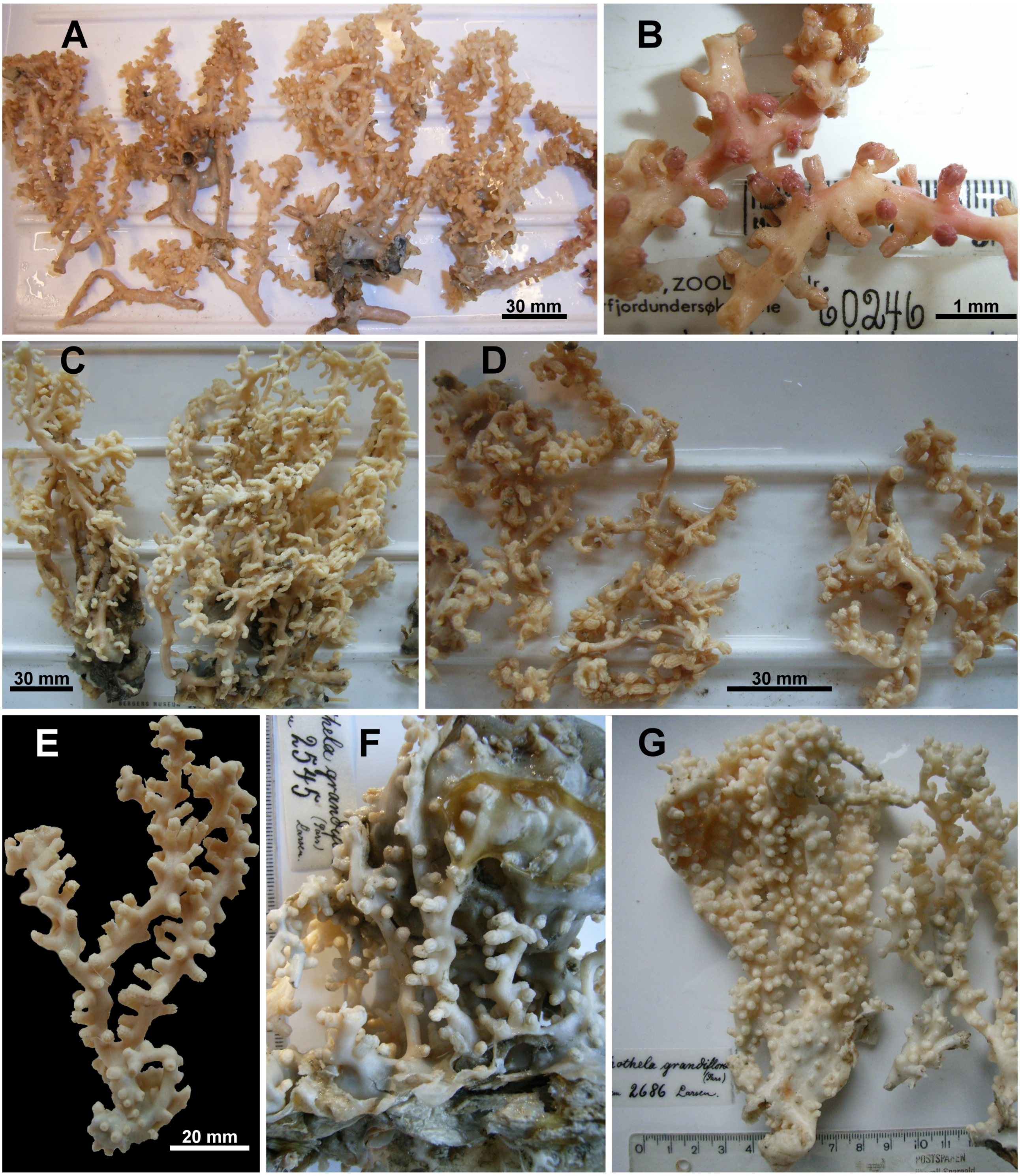

Figure 2.133. *Lateothela anitorkilda,* n.gen., n. sp., paratypes: A-B. ZMUB 60246; C. ZMUB 3897; D. ZMUB 17759 (part), *Anthothela grandiflora* on left, *L. anitorkilda* n. gen., n. sp. on right; E. ZMUB 548; F. ZMB 2545; G. ZMB 2686.

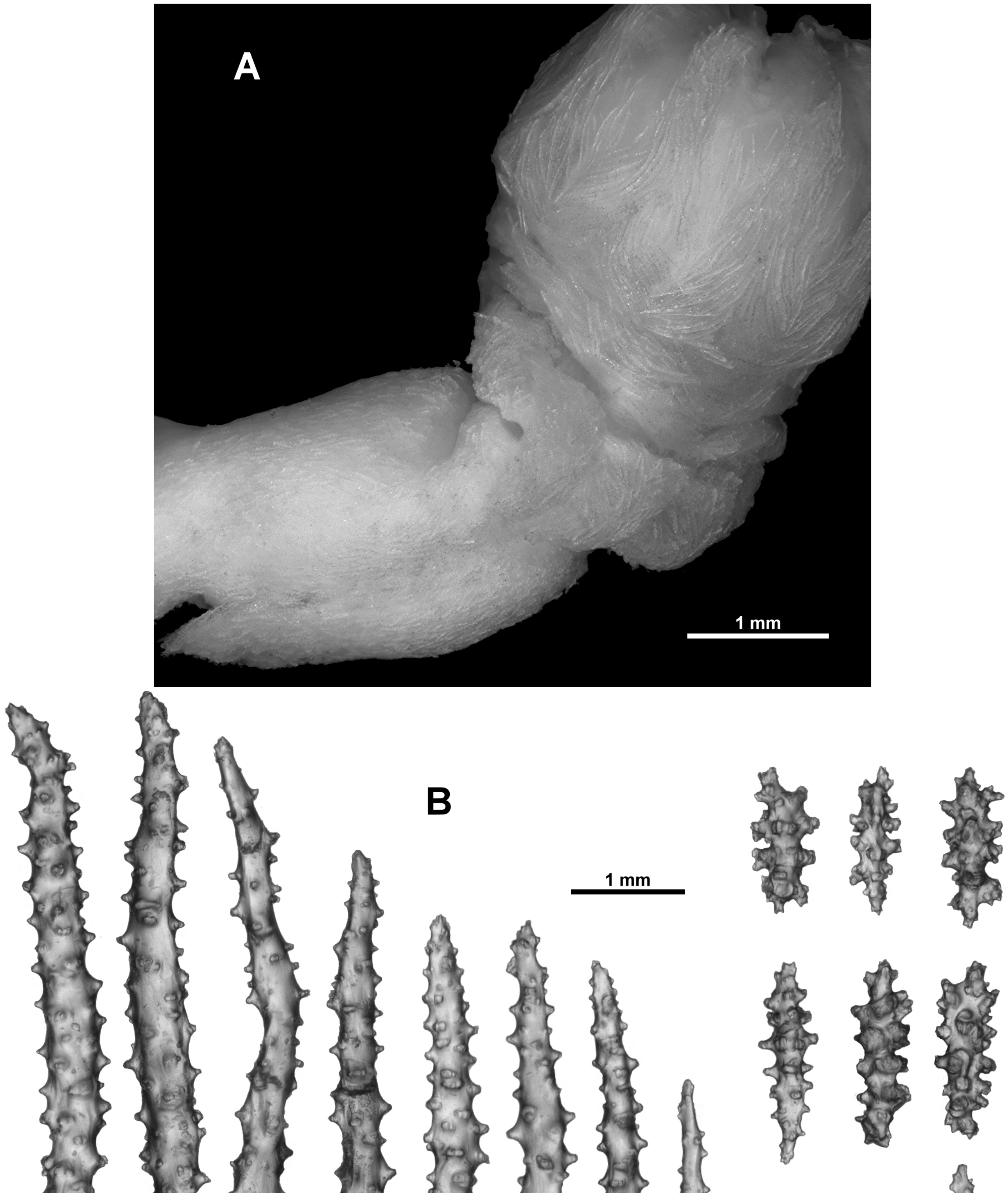

Figure 2.134. *Lateothela anitorkilda,* n. gen., n. sp., ZMUB 12120: A. Polyp; B. Calyx sclerites.

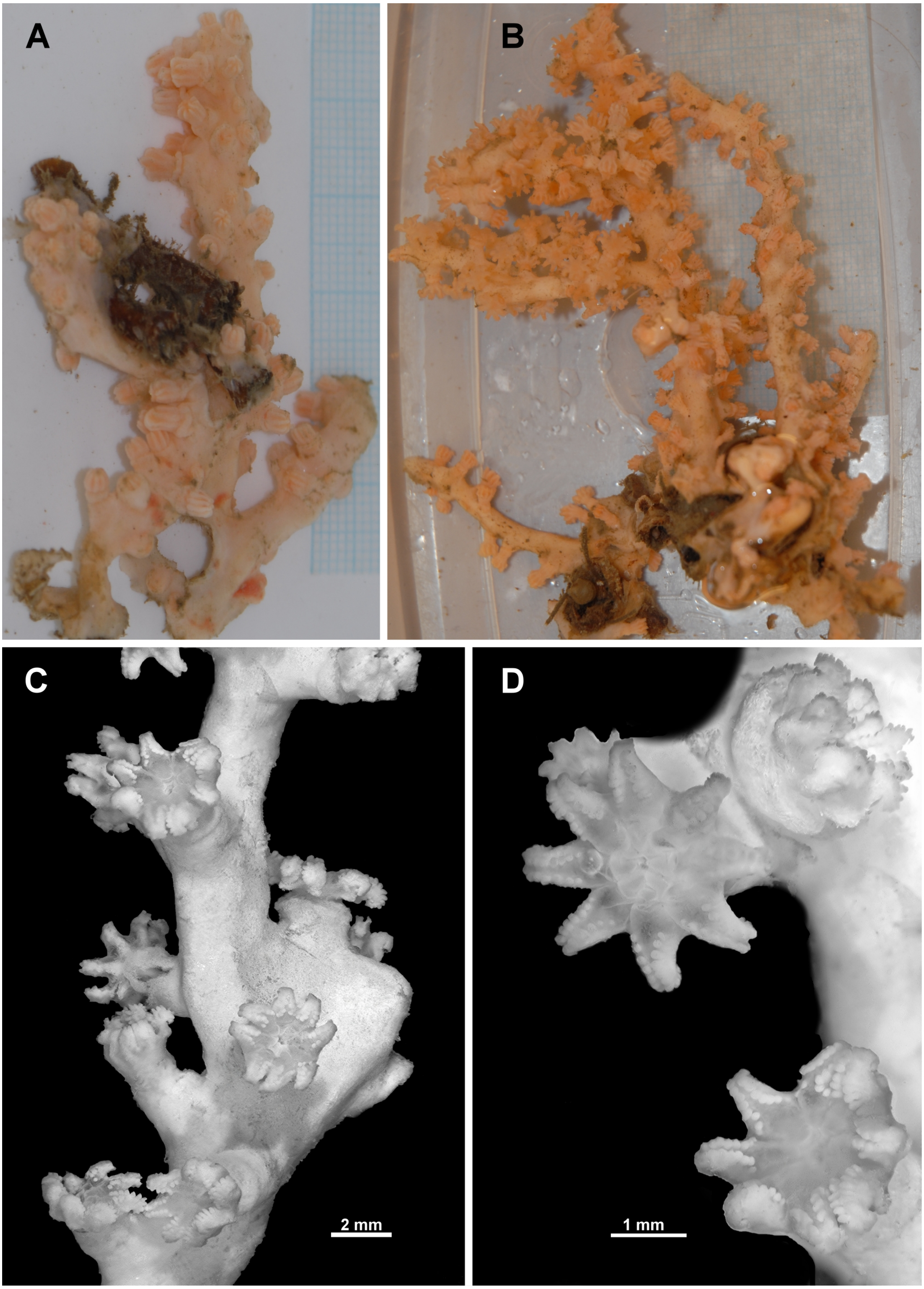

Figure 2.135. *Lateothela anitorkilda,* n. gen. n. sp.: A. NTNU 67147: B-D. NTNU 68106: (B). Recently collected colony; C. Branch; D. Open polyps. (A-B. Courtesy of Torkild Bakken, NTNU).

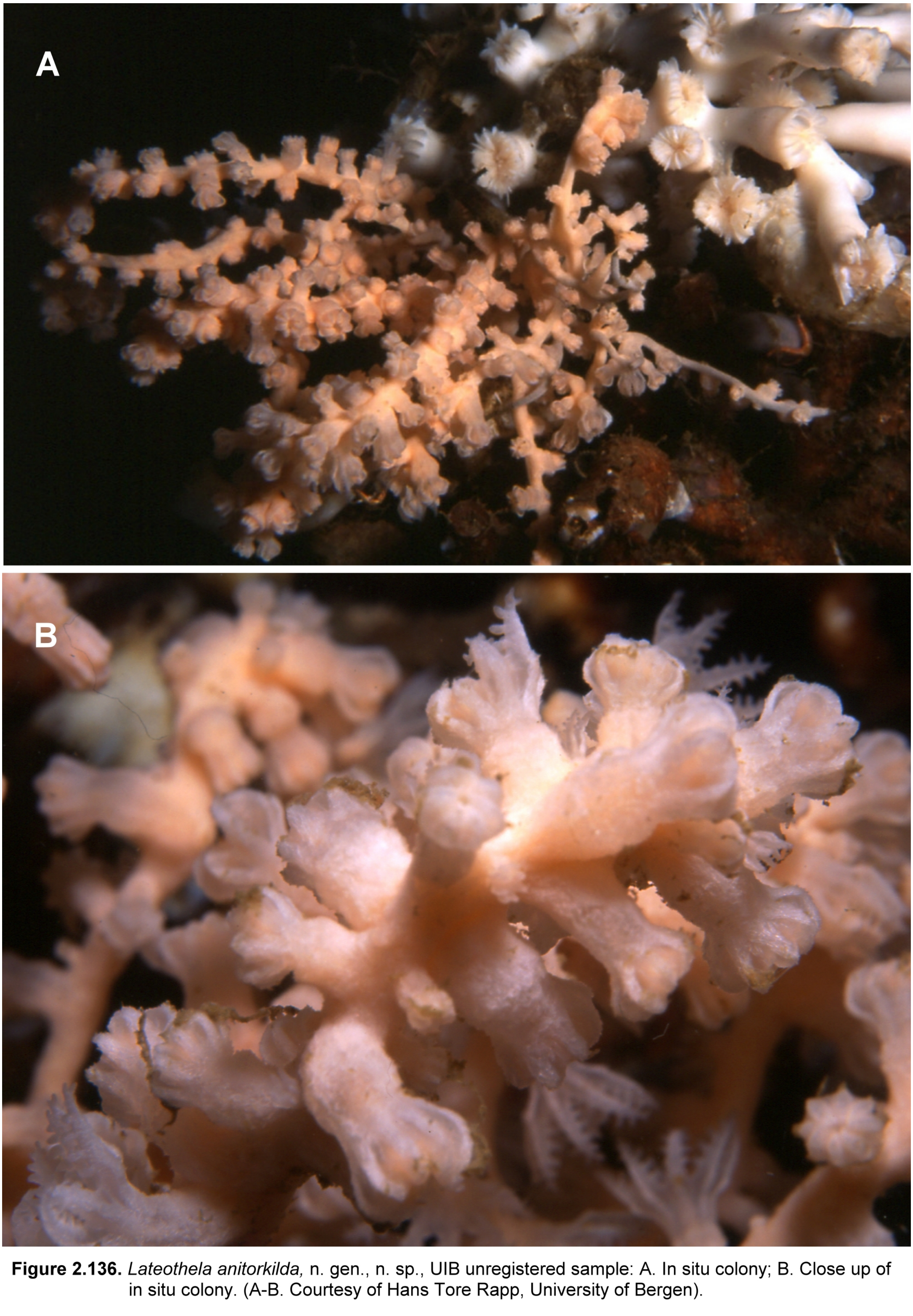

Figure 2.136. *Lateothela anitorkilda,* n. gen., n. sp., UIB unregistered sample: A. In situ colony; B. Close up of in situ colony. (A-B. Courtesy of Hans Tore Rapp, University of Bergen).

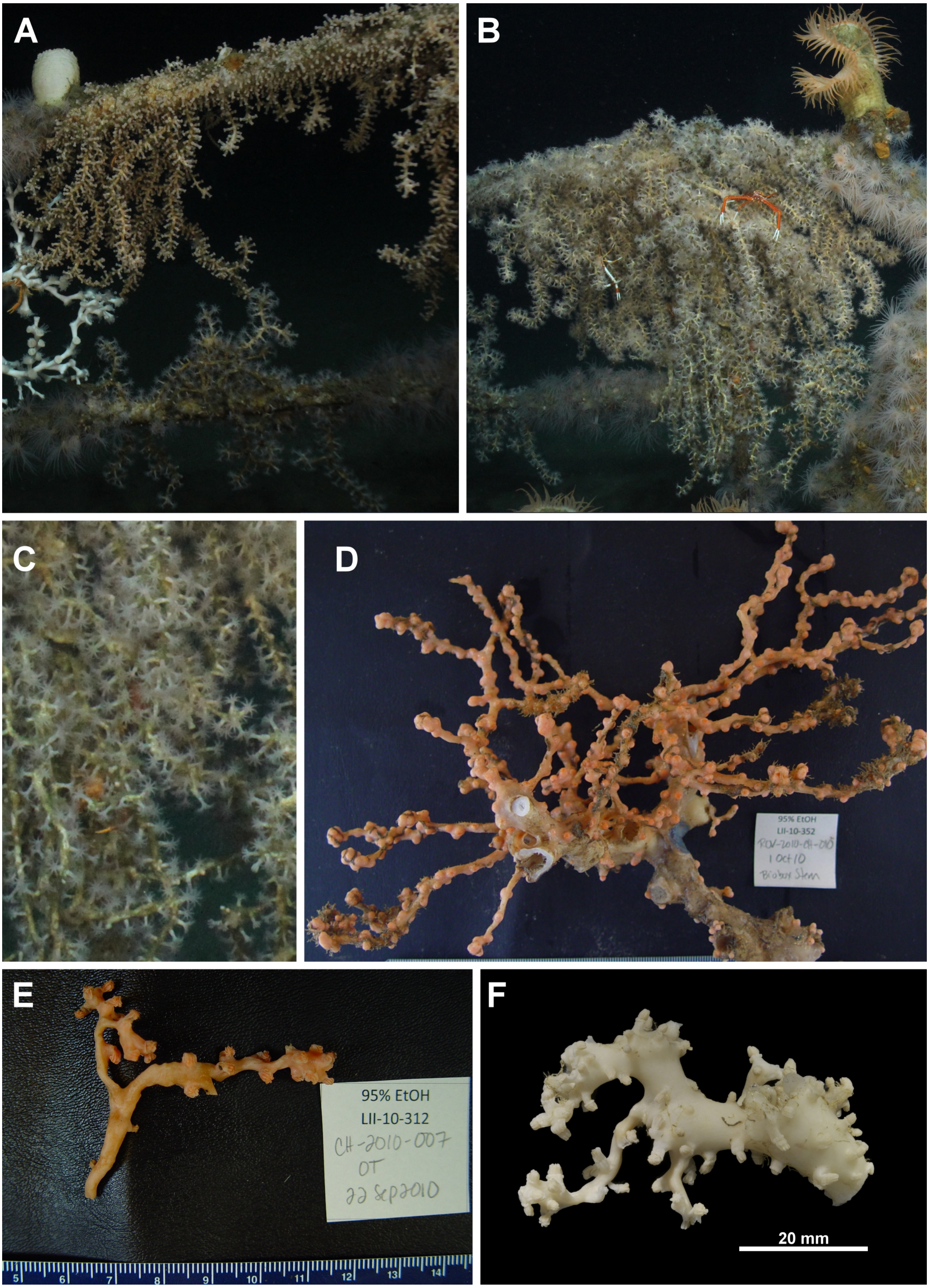

Figure 2.137. *Lateothela anitorkilda,* n.gen. n. sp: A. TMAG K4272; B-D. USNM 1207953: (B). In situ colony; (C). In situ colony with extended tentacles; (D). Recently collected colony; E. USNM 1207952; F. USNM 1139021.

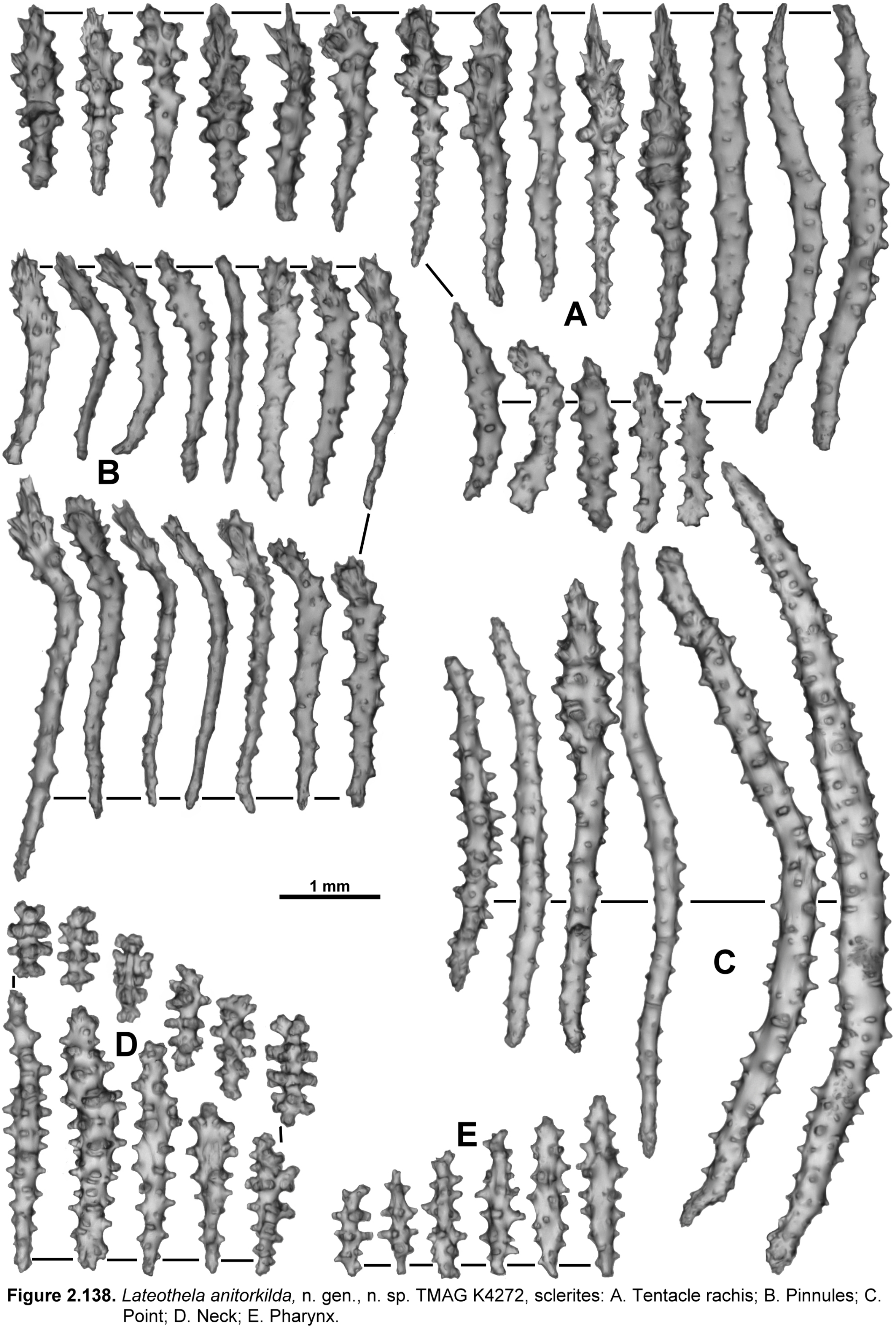

Figure 2.138. *Lateothela anitorkilda,* n. gen., n. sp. TMAG K4272, sclerites: A. Tentacle rachis; B. Pinnules; C. Point; D. Neck; E. Pharynx.

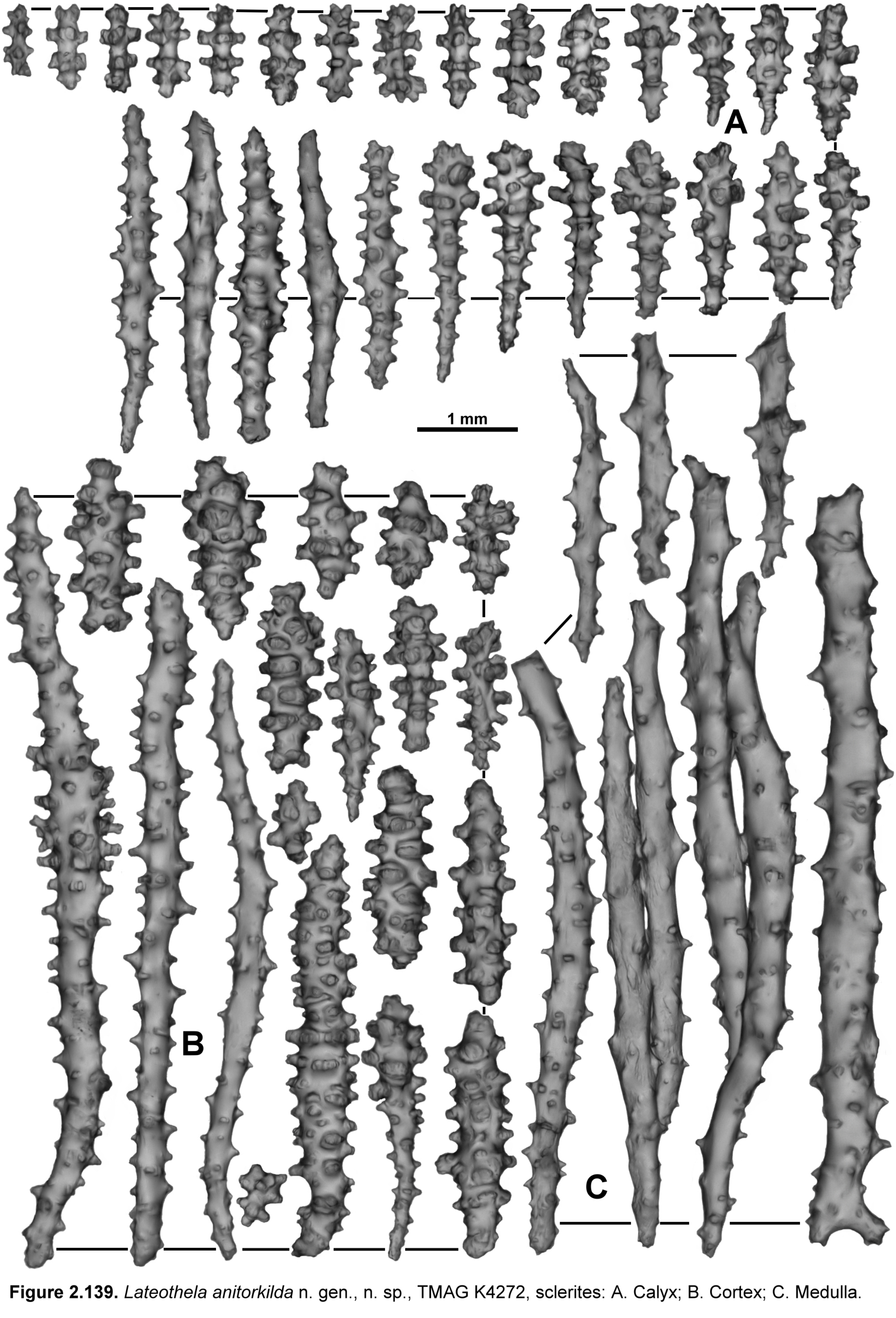

Figure 2.139. *Lateothela anitorkilda* n. gen., n. sp., TMAG K4272, sclerites: A. Calyx; B. Cortex; C. Medulla.

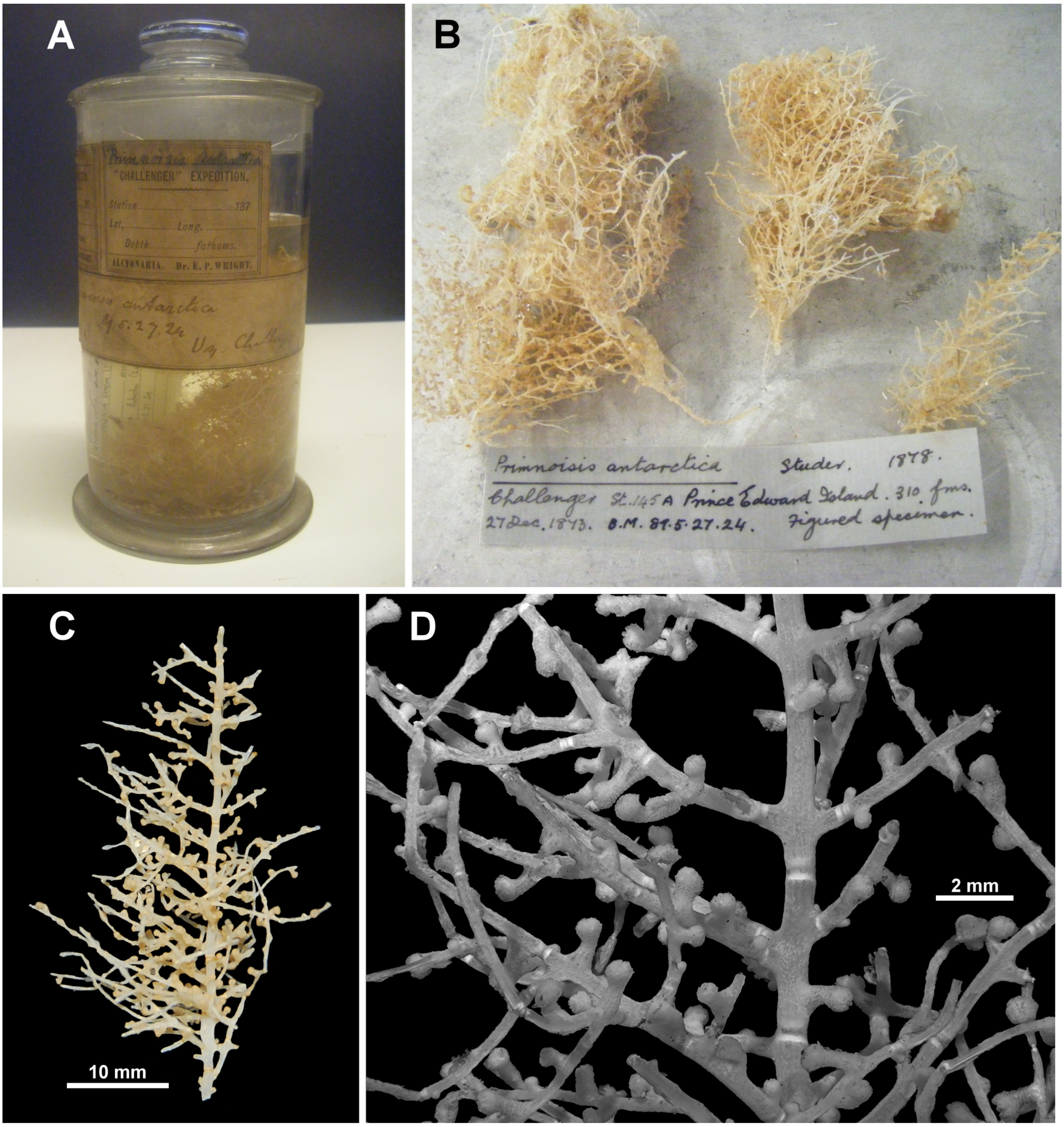

Figure 3.1. *Primnoisis antarctica* Wright & Studer,1889, holotype: A-B. Holotype lot; C. Fragment examined; D. Branch and polyp arrangement. (A-B. Courtesy of NHMUK stafff).

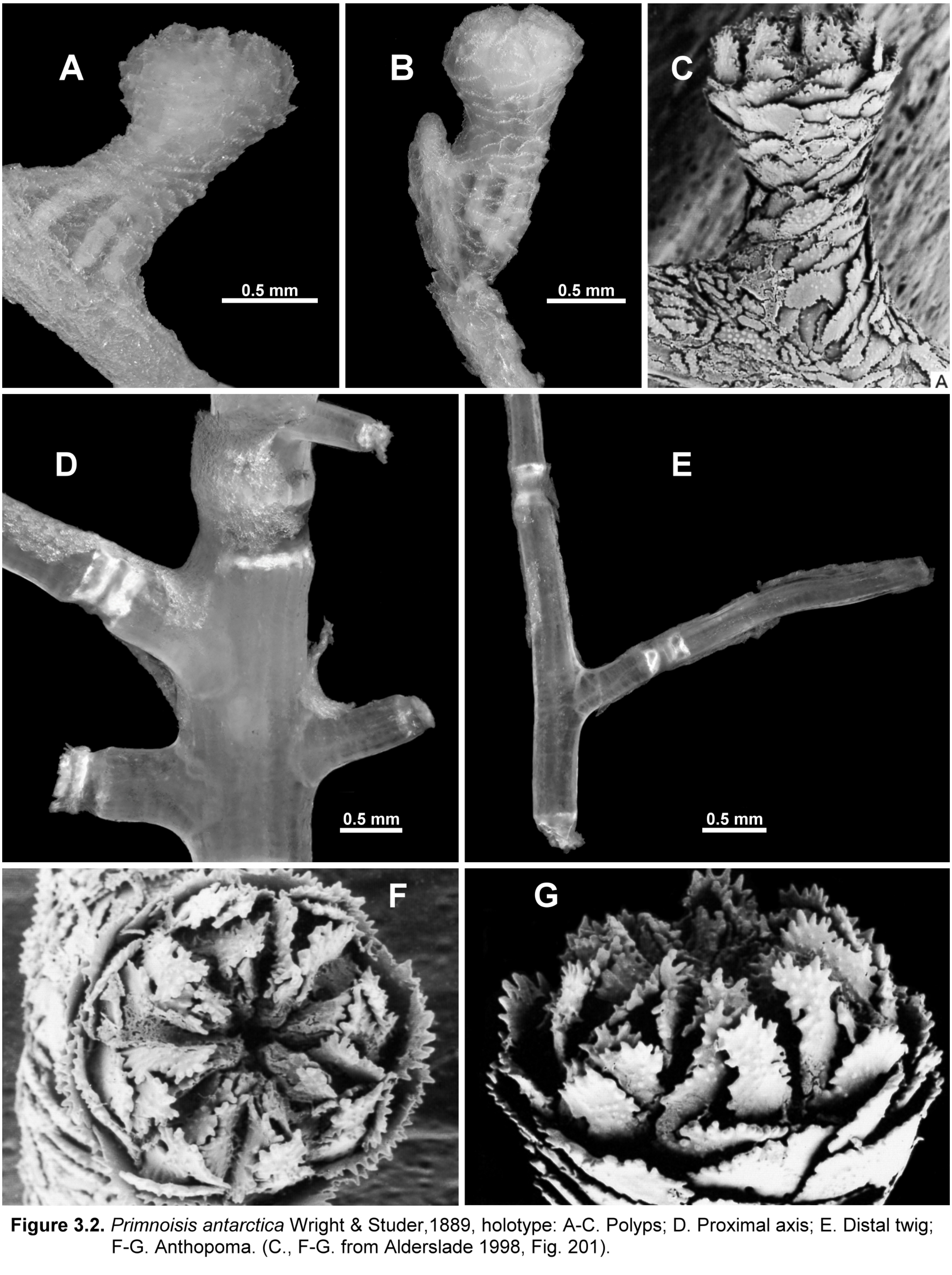

Figure 3.2. *Primnoisis antarctica* Wright & Studer,1889, holotype: A-C. Polyps; D. Proximal axis; E. Distal twig; F-G. Anthopoma. (C., F-G. from Alderslade 1998, Fig. 201).

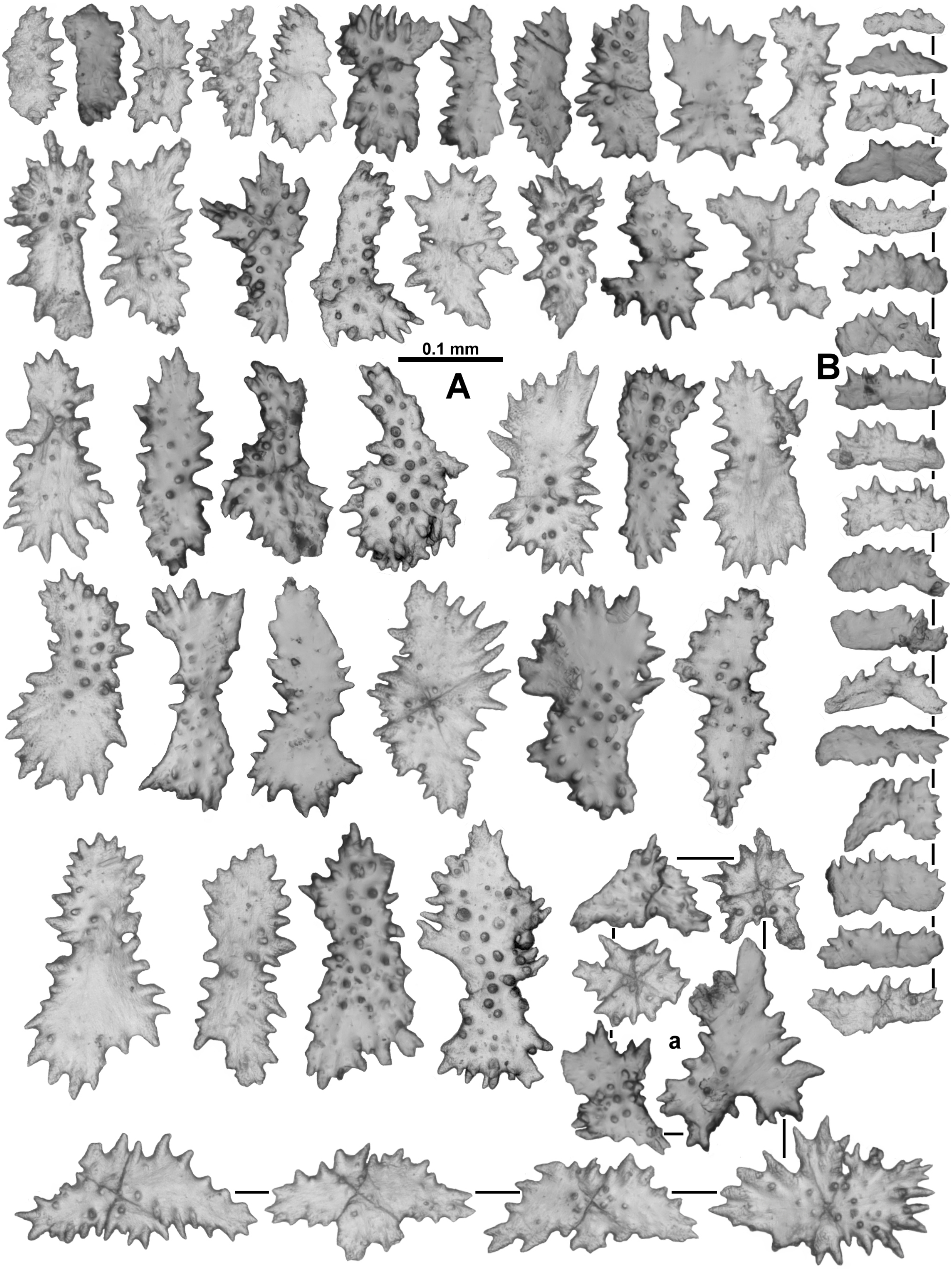

Figure 3.3. *Primnoisis antarctica* Wright & Studer,1889, holotype, sclerites: A. Anthopoma (a. irregular sclerites from transition region); B. Tentacle.

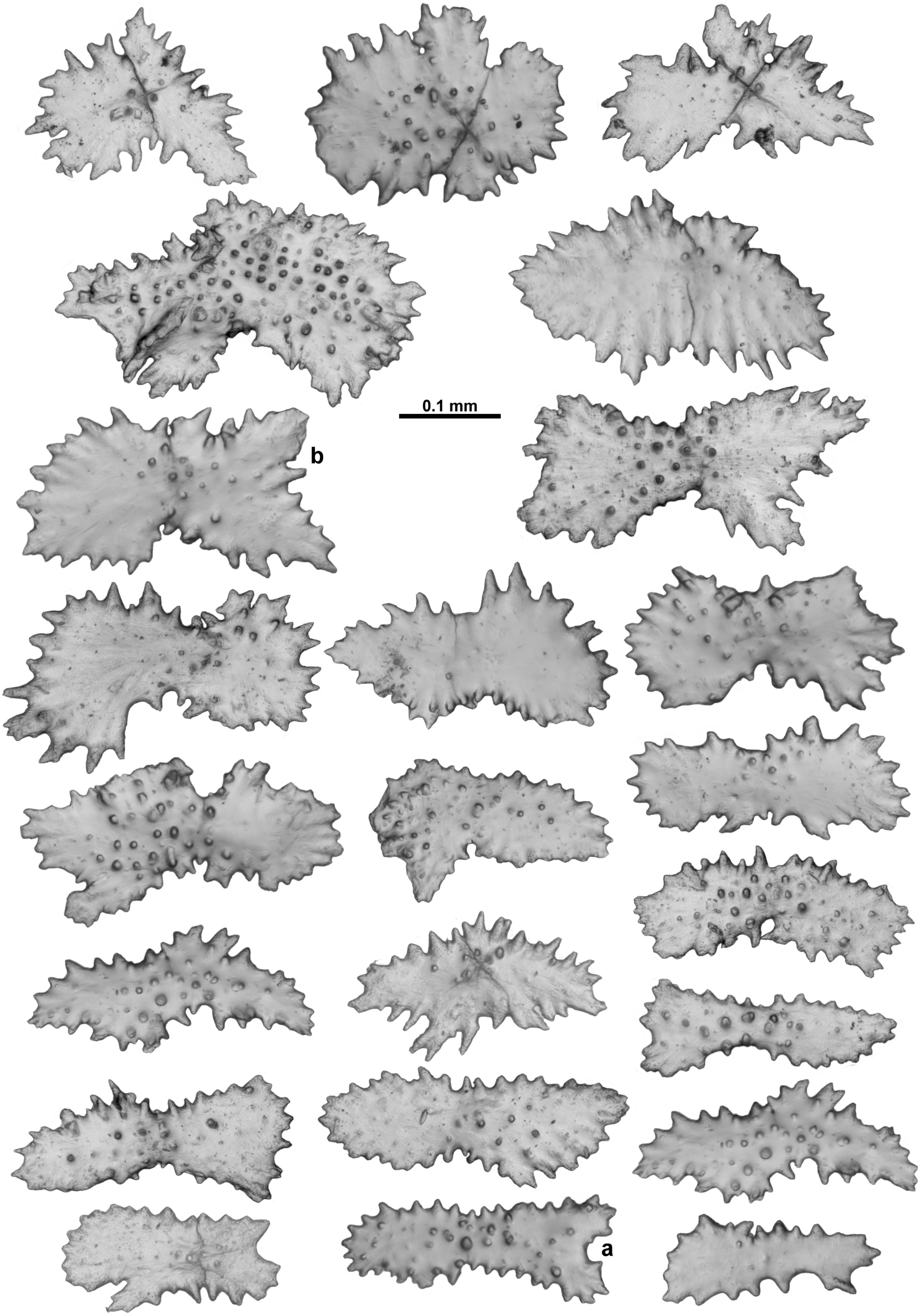

Figure 3.4. *Primnoisis antarctica* Wright & Studer,1889, holotype, sclerites: Polyp body (a. narrow sclerite from polyp base; b. lobed sclerite with indented base).

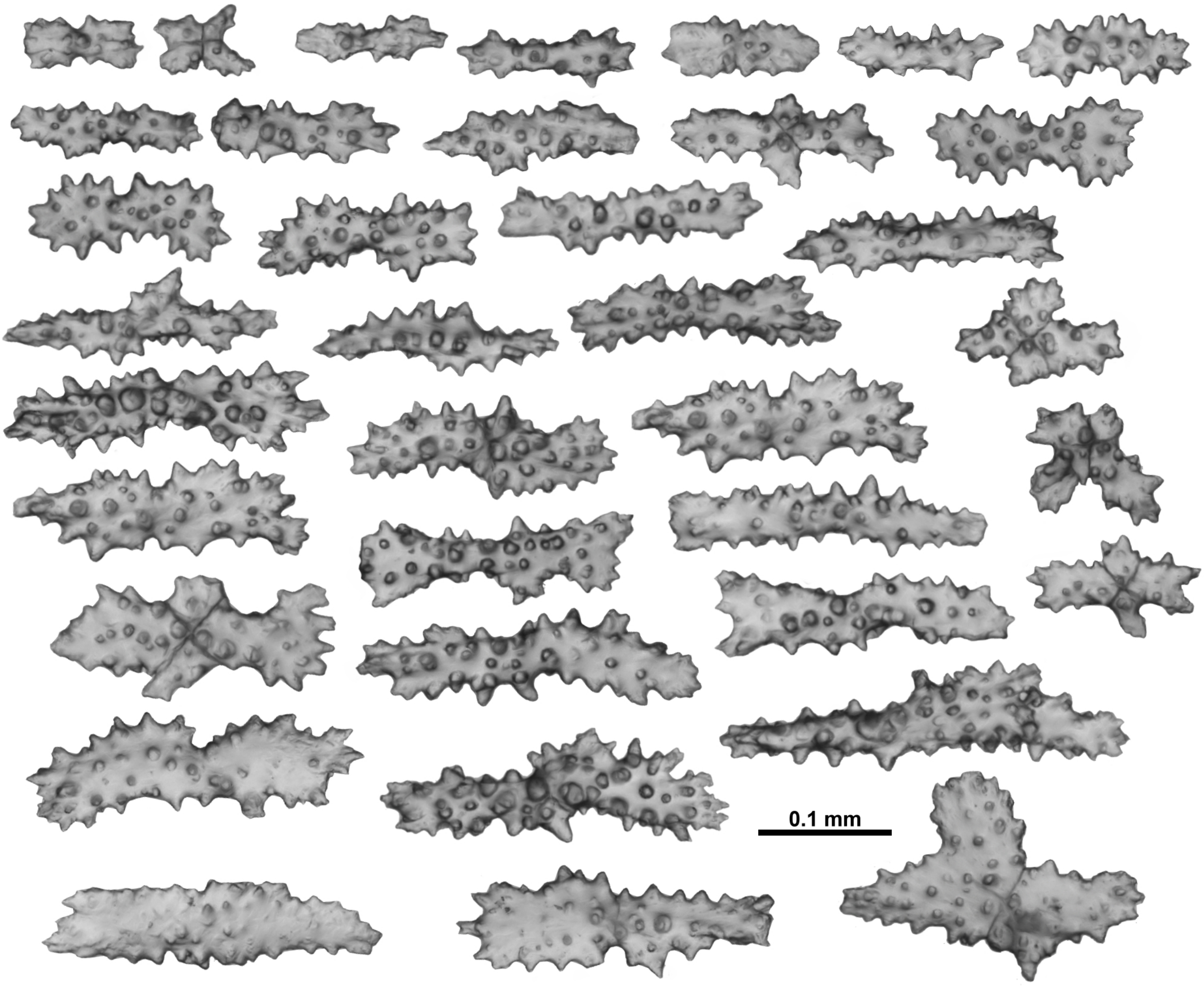

Figure 3.5. *Primnoisis antarctica* Wright & Studer,1889, holotype, sclerites: Branch coenenchyme.

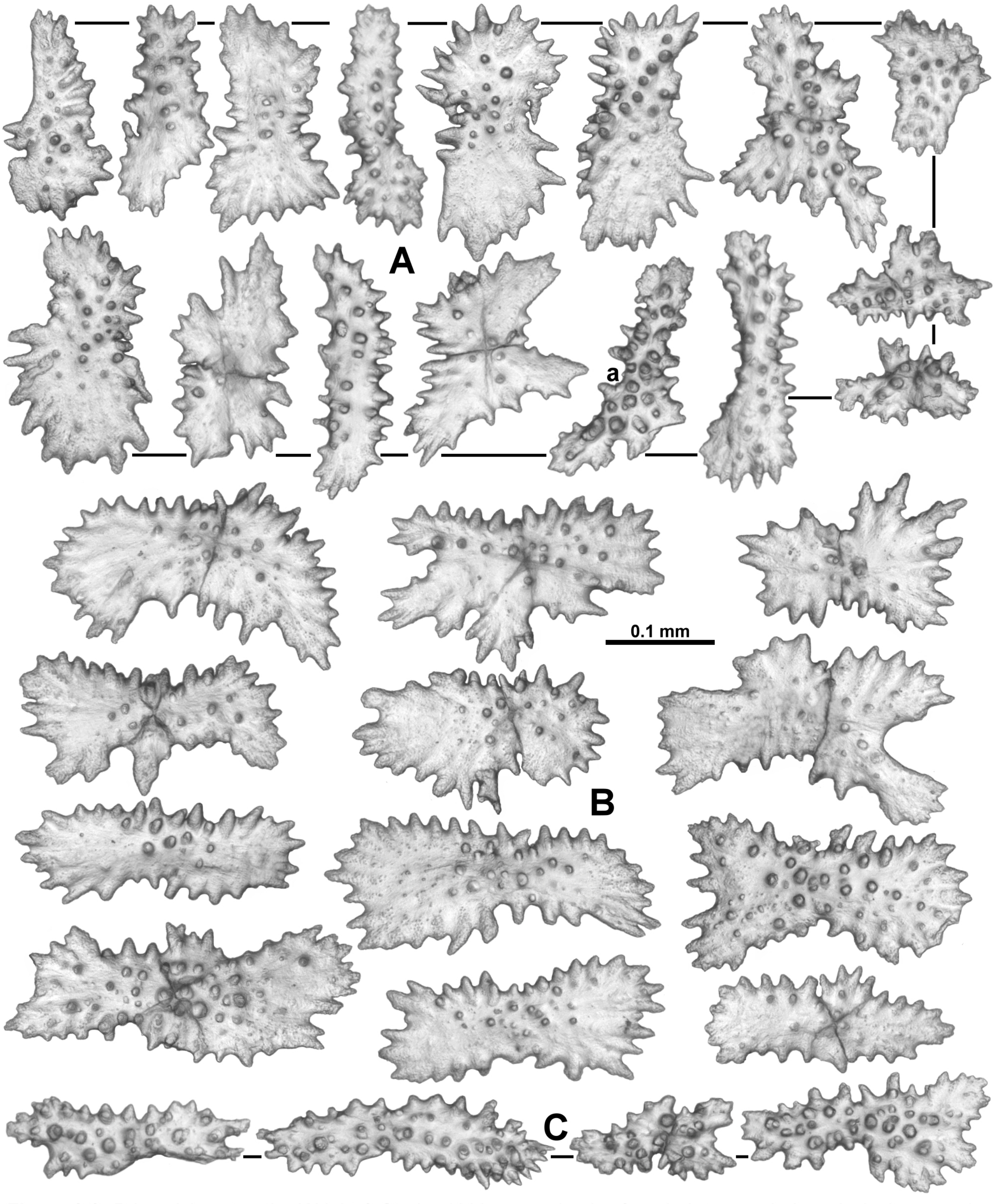

Figure 3.6. *Primnoisis antarctica* Wright & Studer,1889, second polyp from holotype, sclerites: A. Anthopoma (a. tuberculate rod); B. Polyp body; C. Branch coenenchyme.

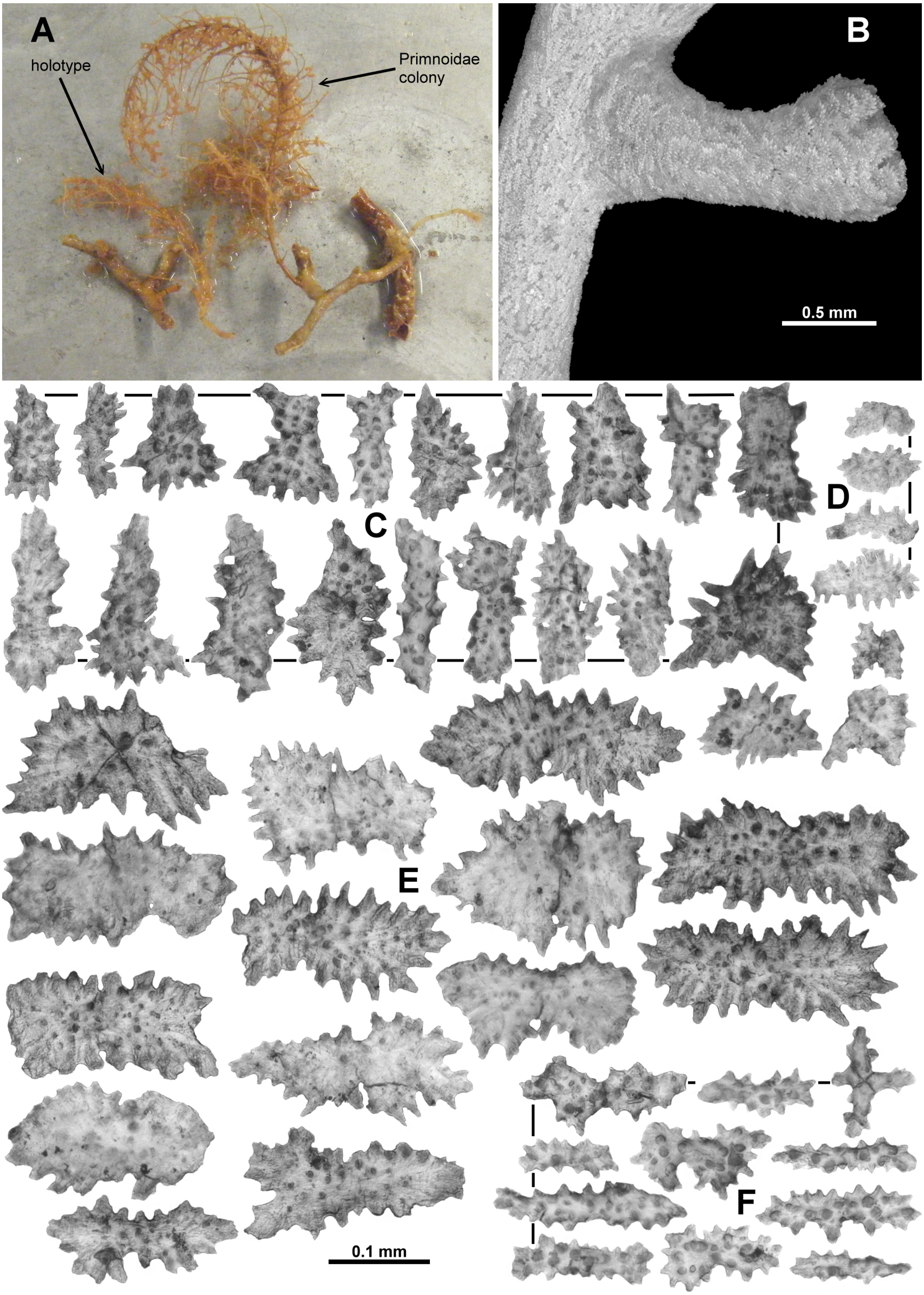

Figure 3.7. *Primnoisis sparsa* Wright & Studer,1889, holotype : A. Colony; B. Polyp; C. Anthopomal sclerites; D. Tentacular sclerites; E. Polyp body sclerites; F. Surface sclerites. (A. Courtesy of NHMUK staff).

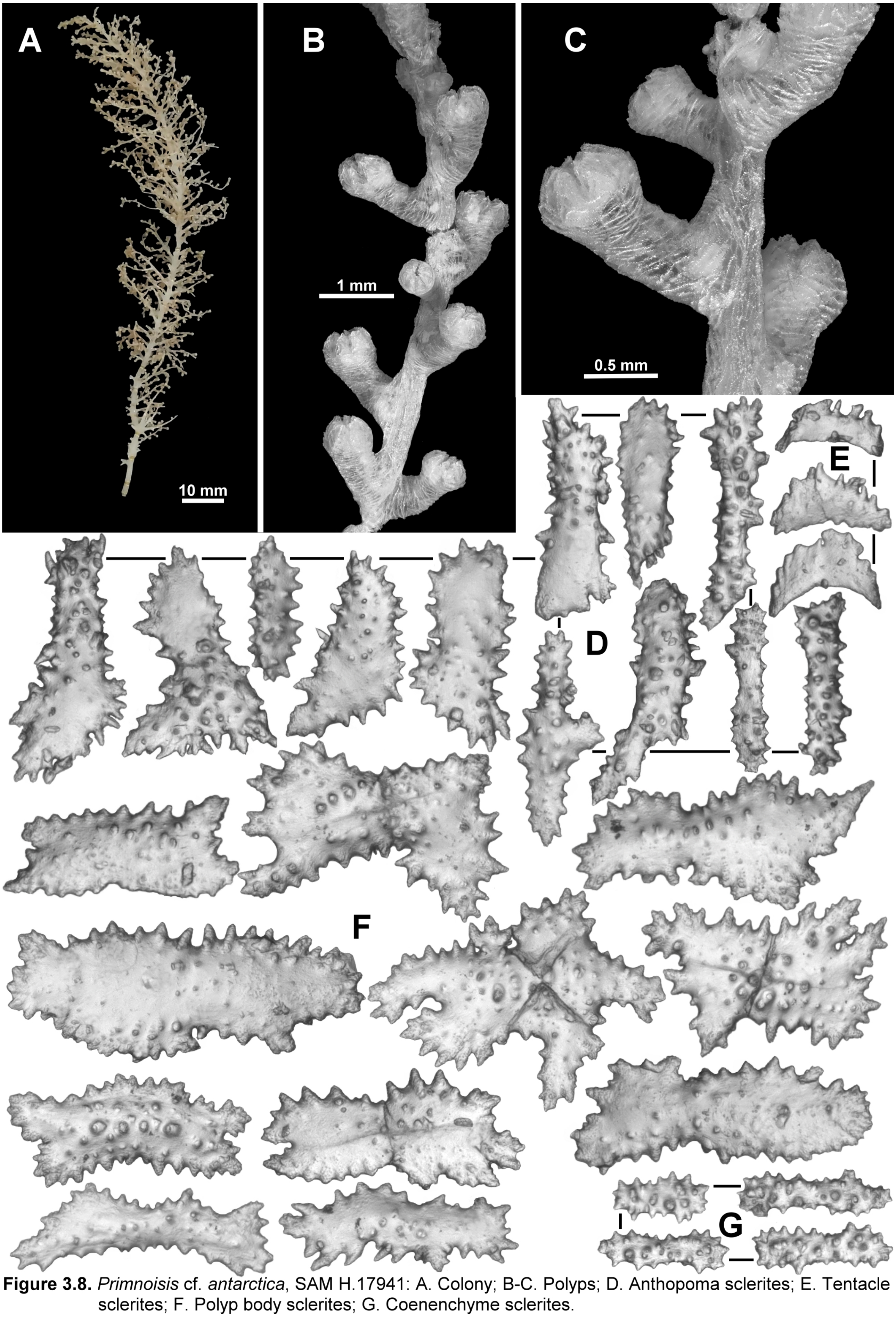

Figure 3.8. *Primnoisis* cf. *antarctica*, SAM H.17941: A. Colony; B-C. Polyps; D. Anthopoma sclerites; E. Tentacle sclerites; F. Polyp body sclerites; G. Coenenchyme sclerites.

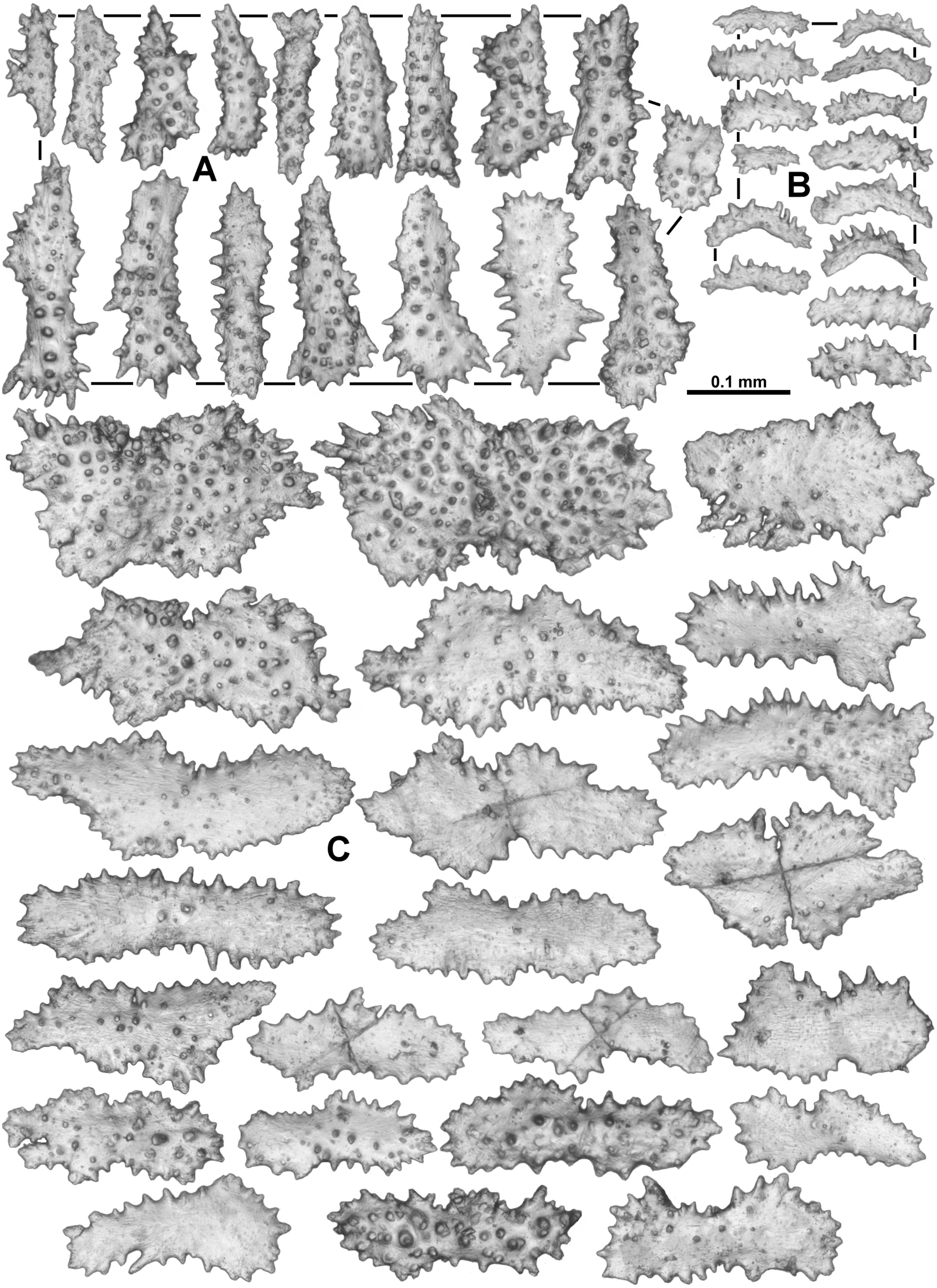

Figure 3.9. *Primnoisis* cf. *antarctica*, G.13236, sclerites: A. Anthopoma; B. Tentacle; C. Polyp body.

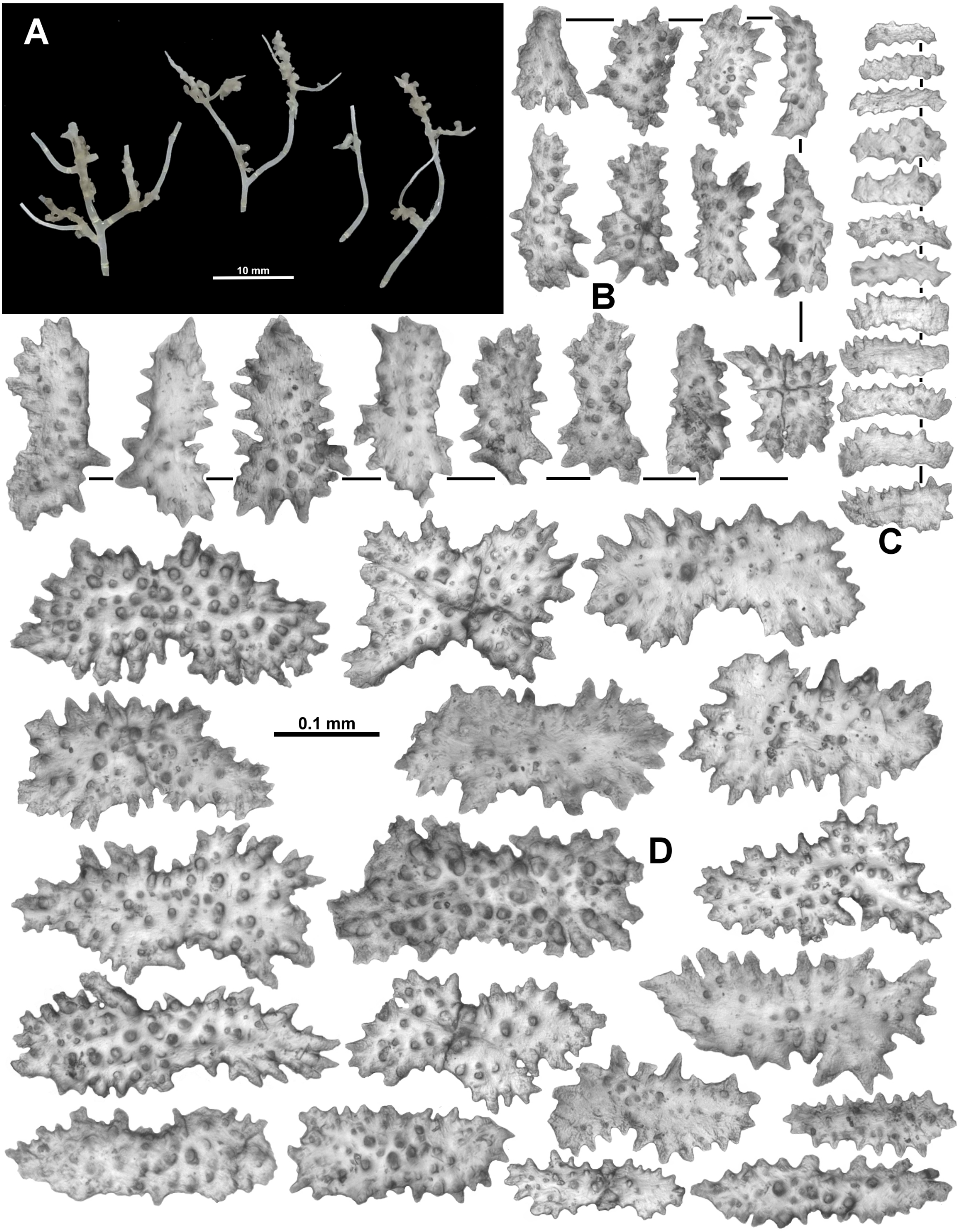

Figure 3.10. *Primnoisis* cf. *antarctica,* SC50 H43: A. Colony fragments; B. Anthopoma sclerites; C. Tentacle sclerites; D. Polyp body sclerites.

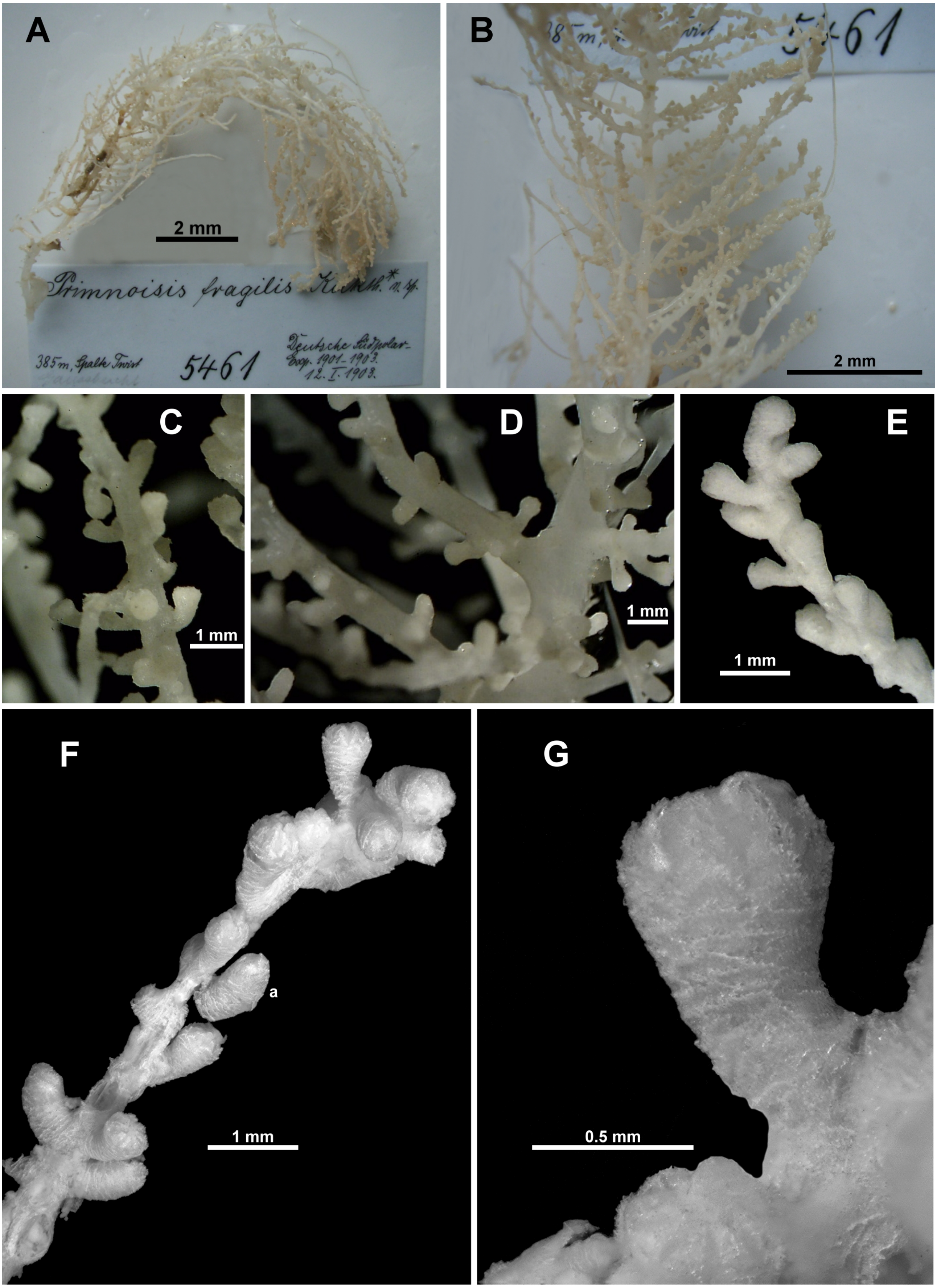

Figure 3.11. *Primnoisis fragilis* Kükenthal, 1912, lectotype: A-B. Colony; C-F. Arrangement of polyps (a. brooding polyp); G. Polyp.

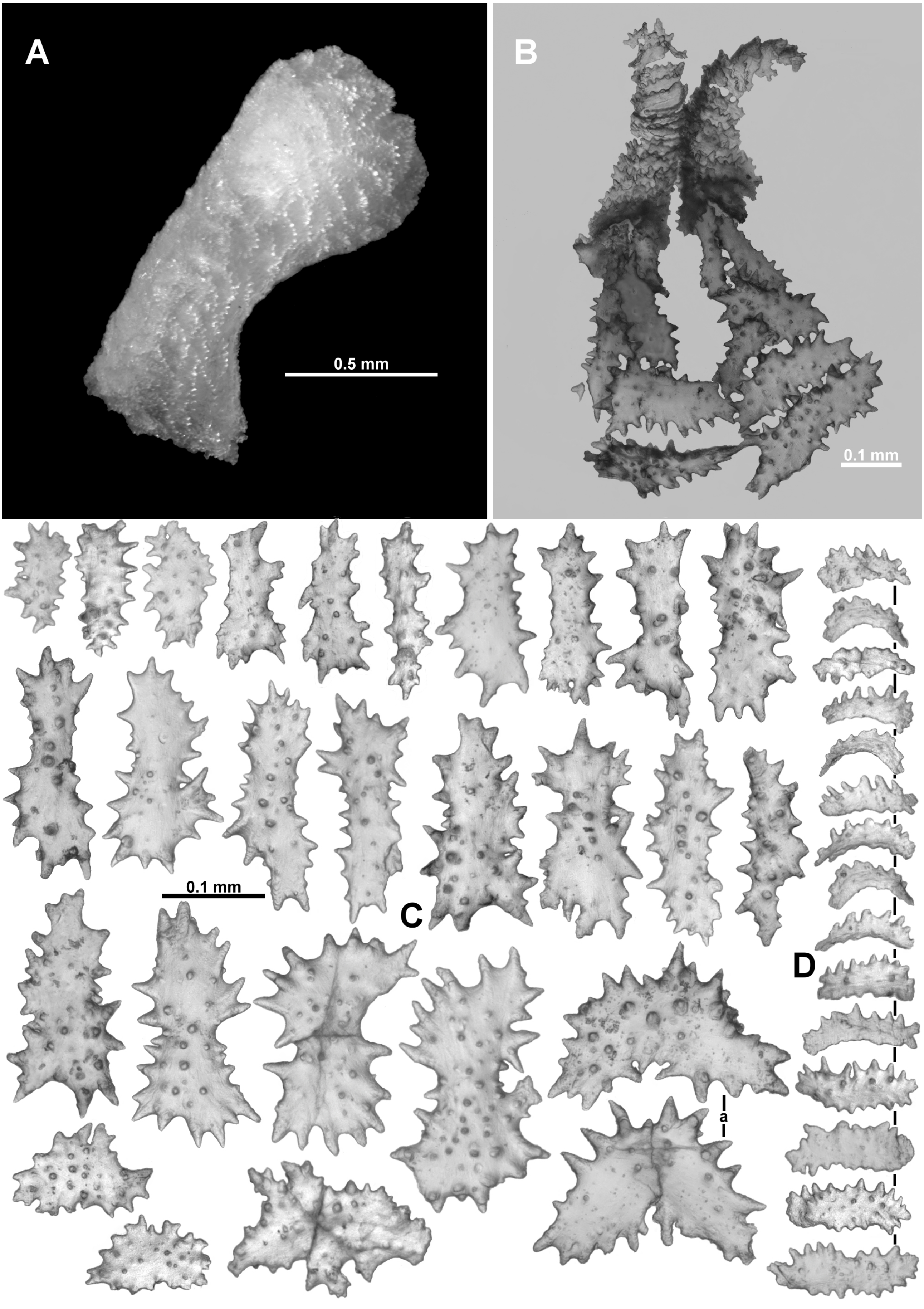

Figure 3.12. *Primnoisis fragilis* Kükenthal, 1912, lectotype: A. Polyp; B. Anthopoma and tentacle sclerites in situ; C. Anthopoma sclerites (a. irregular transition sclerites); D. Tentacle sclerites.

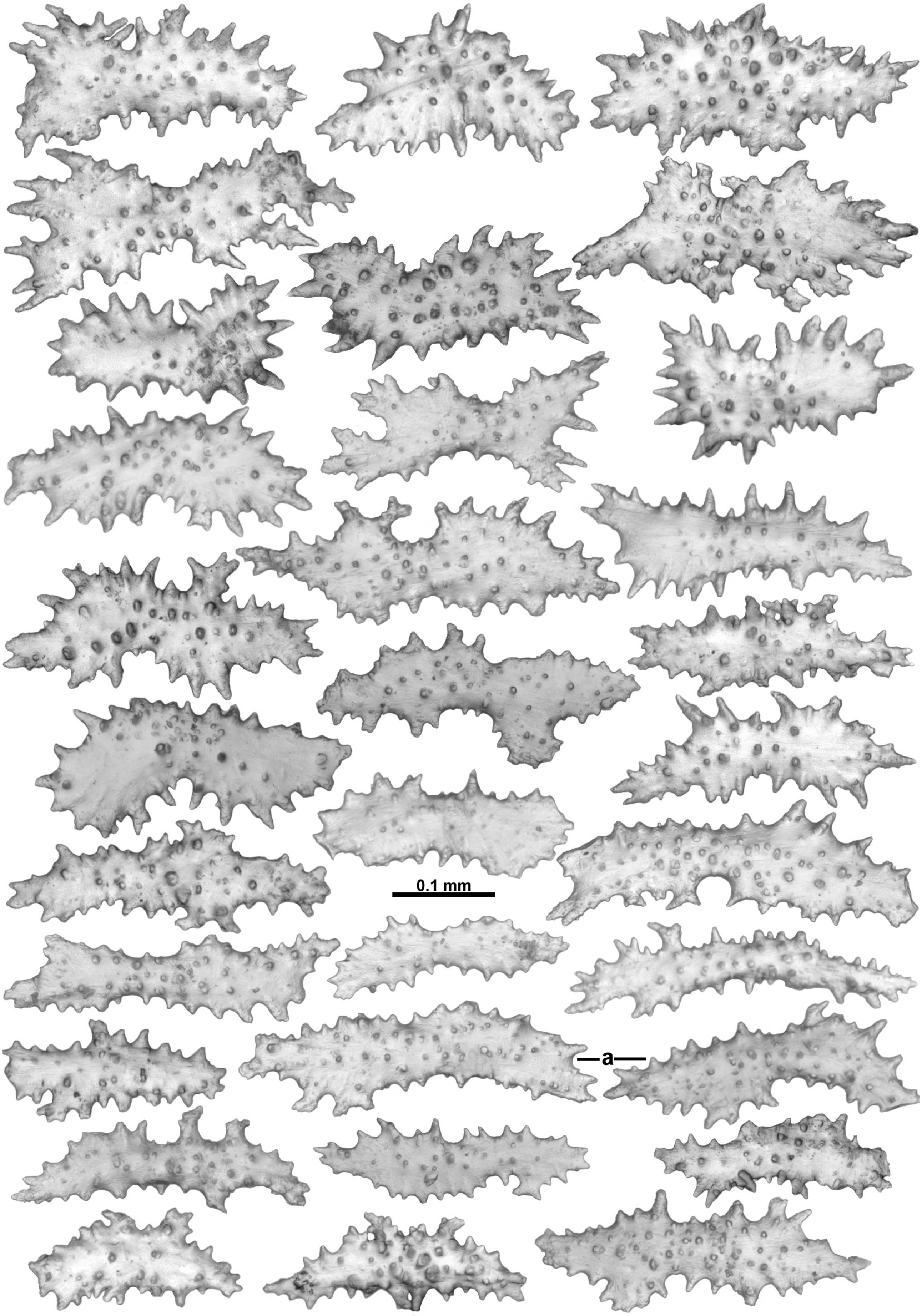

Figure 3.13. *Primnoisis fragilis* Kükenthal, 1912, lectotype, sclerites: Polyp body (a. sclerites from polyp base).

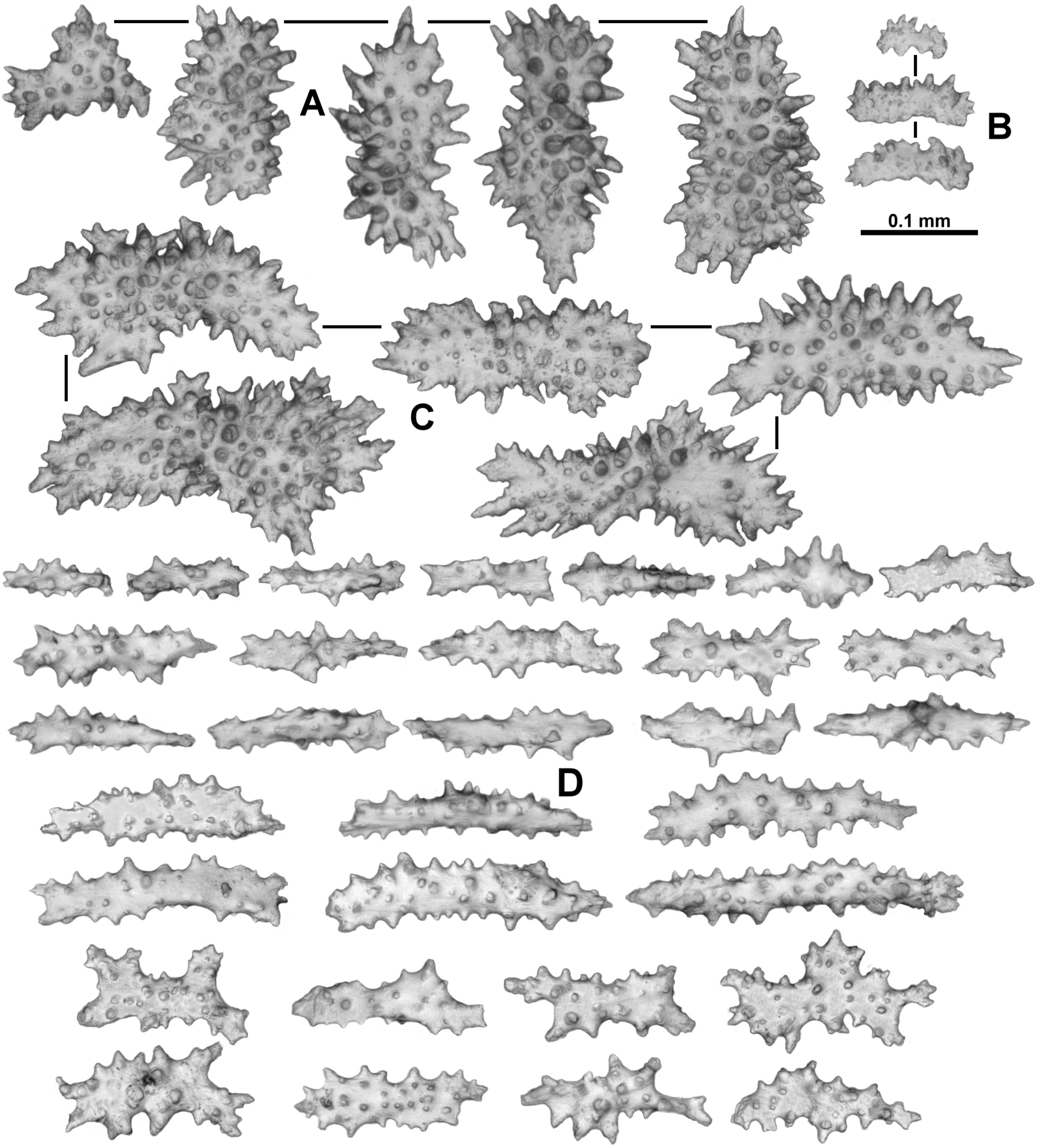

Figure 3.14. *Primnoisis fragilis* Kükenthal, 1912, lectotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body; D. Twig coenenchyme.

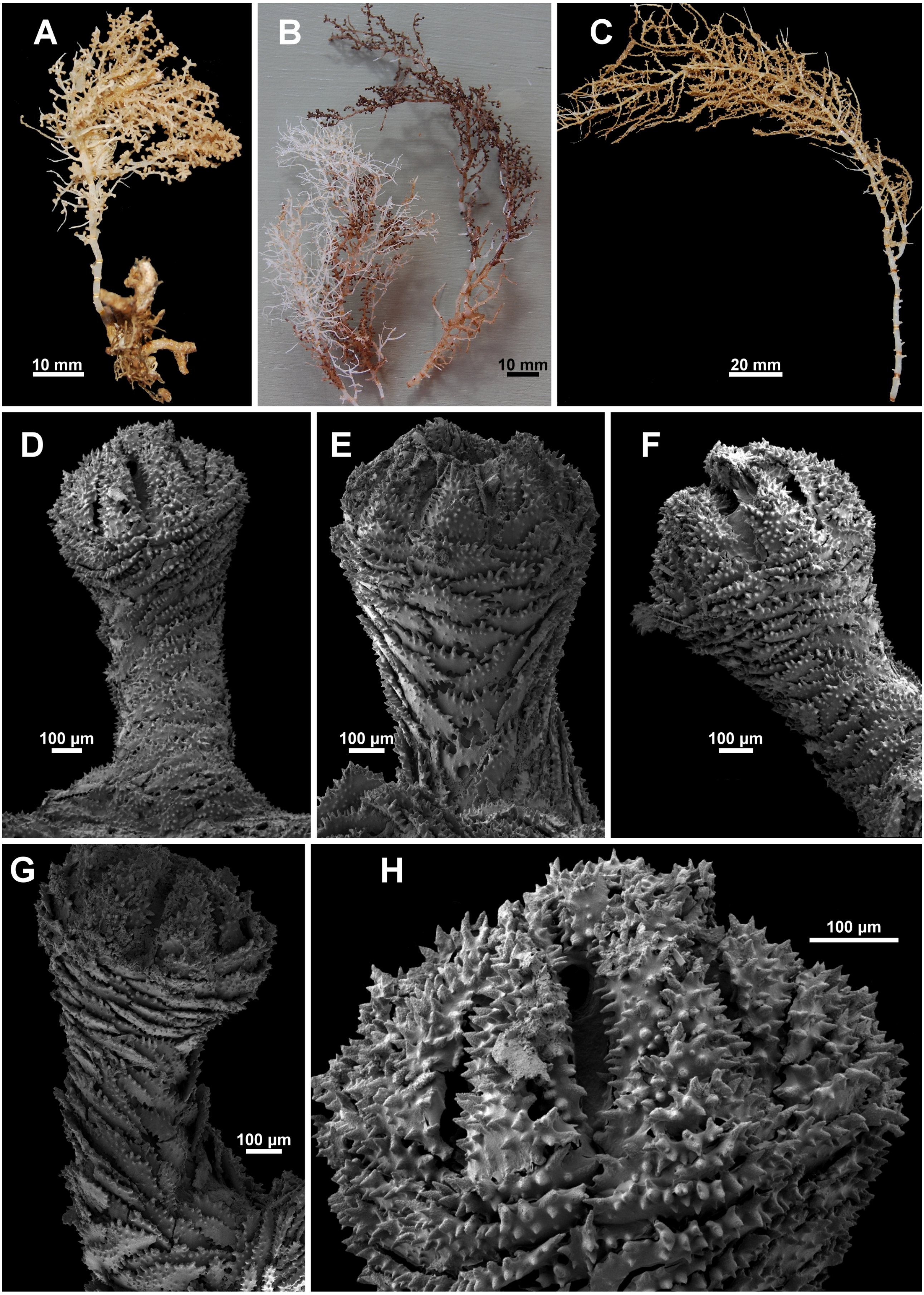

Figure 3.15. *Primnoisis fragilis* Kükenthal, 1912: A., D-F., H. K4295: (A). Colony; (D-F). Polyps; (H). Anthopoma. B., G. K4291: (B). Colony; (G). Polyp. C. MNHN IK-2009-342.

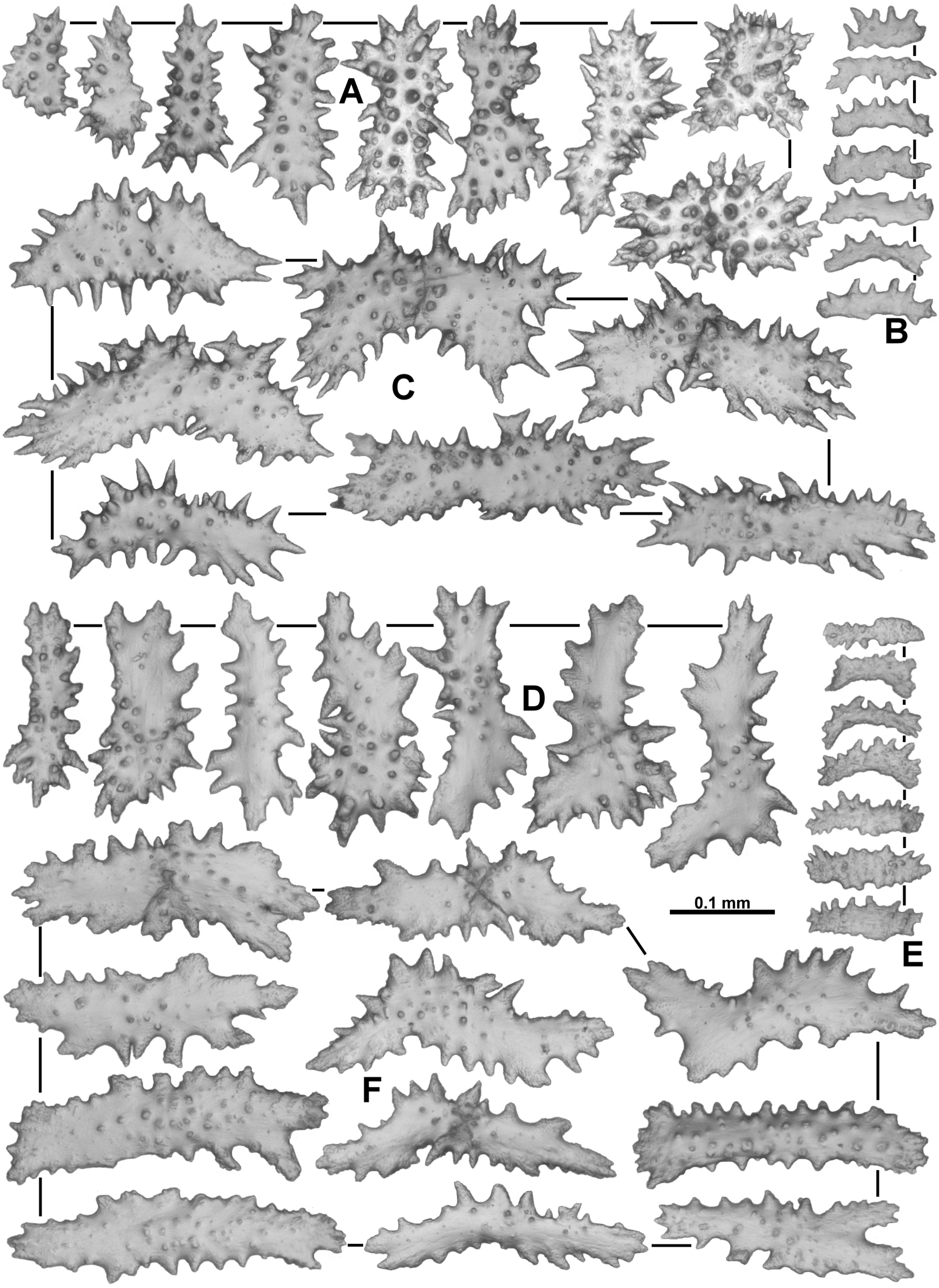

Figure 3.16. *Primnoisis fragilis* Kükenthal, 1912, sclerites: A-C. K4295: (A). Anthopoma; (B). Tentacle; (C). Polyp body. D-F. NIWA 37677: (D). Anthopoma; (E). Tentacle; (F). Polyp body.

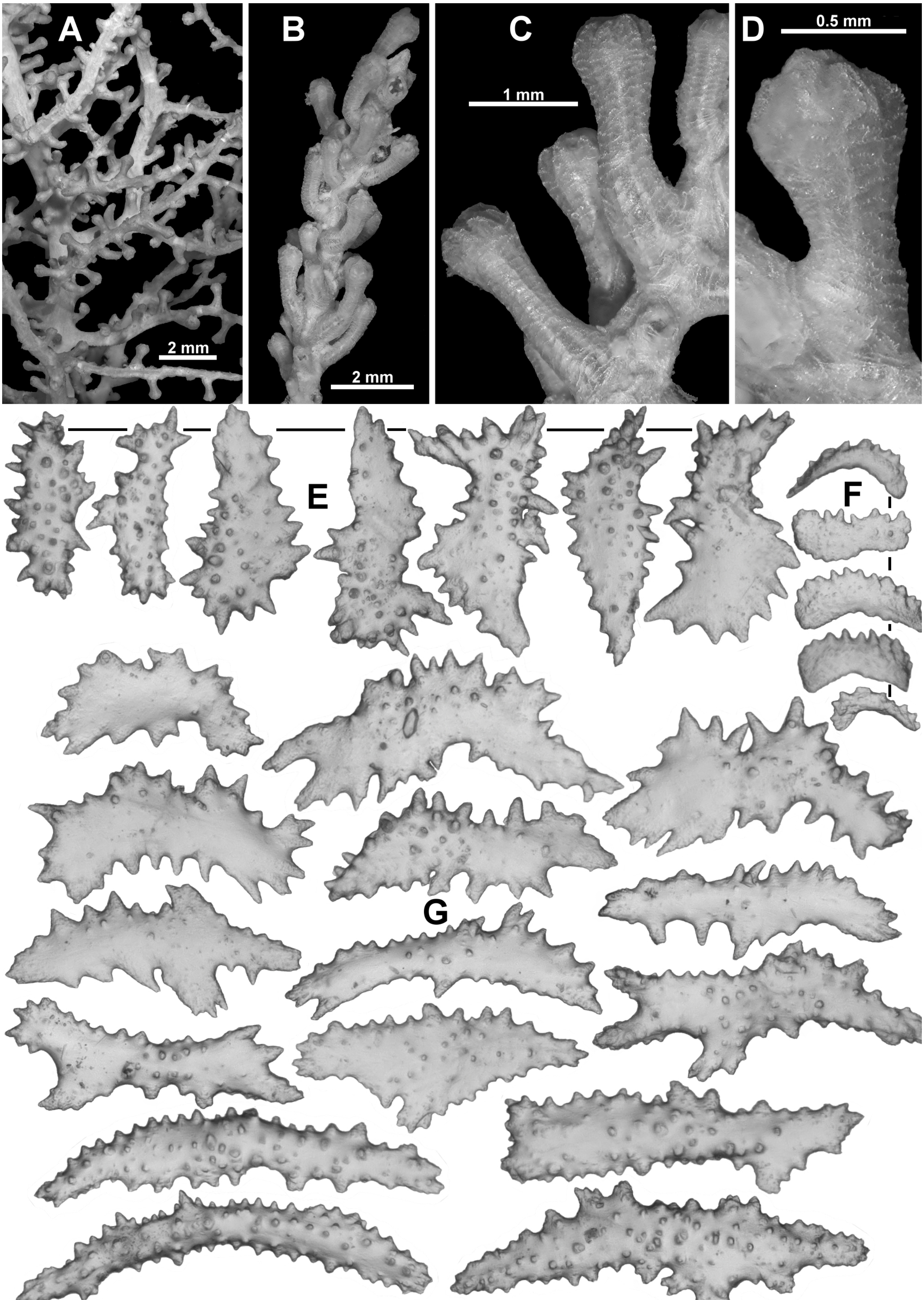

Figure 3.17. *Primnoisis fragilis* Kükenthal, 1912, MNHN IK-2009-342: A. Branching; B. Polyp arrangement at a branch tip; C-D. Polyps; E. Anthopoma sclerites; F. Tentacle sclerites; G. Polyp body sclerites.

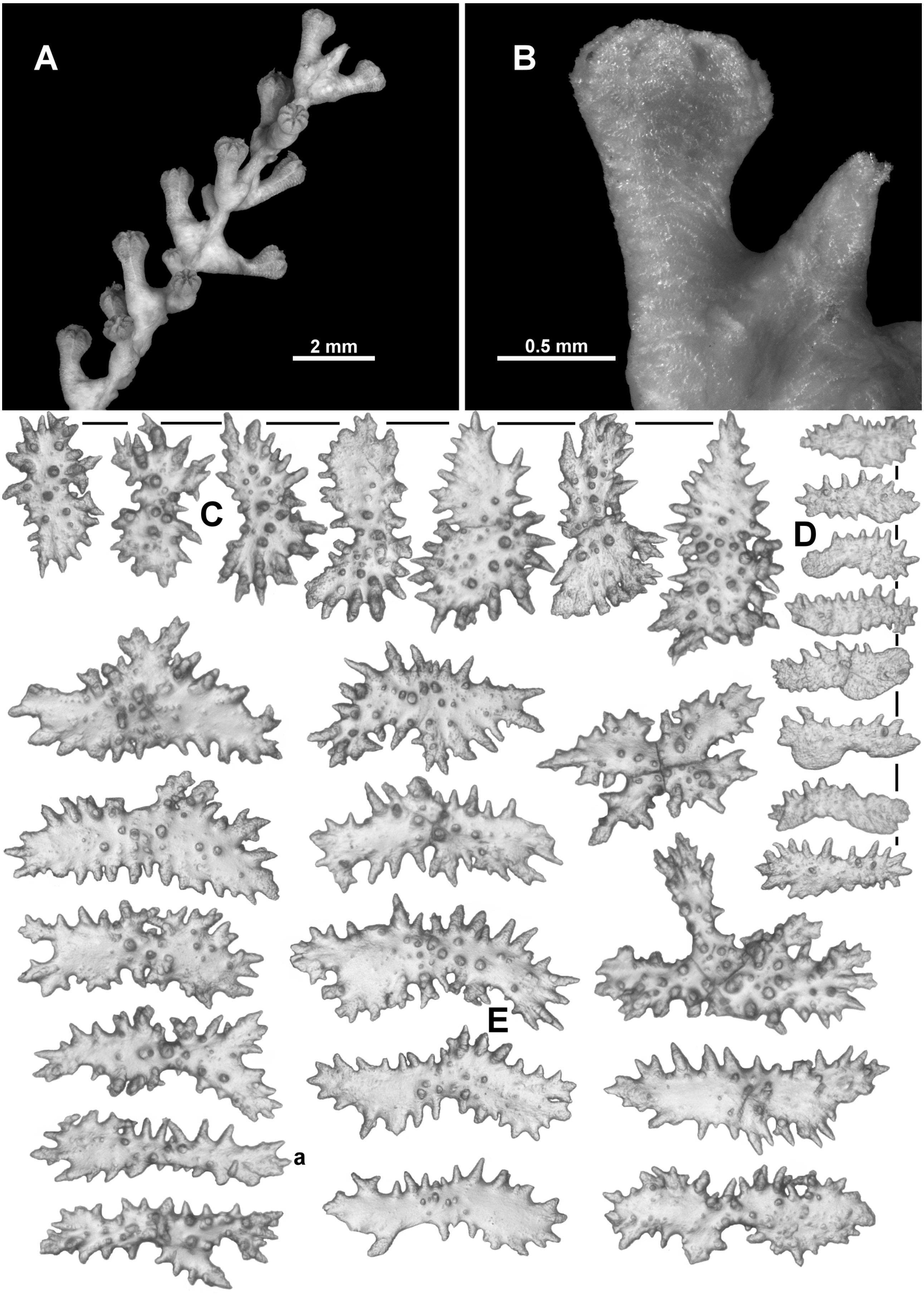

Figure 3.18. *Primnoisis fragilis* Kükenthal, 1912, SIO Co2479: A. Polyp arrangement; B. Polyp; C. Anthopoma sclerites; D. Tentacle sclerites; E. Polyp body sclerites (a. sclerite from near polyp base).

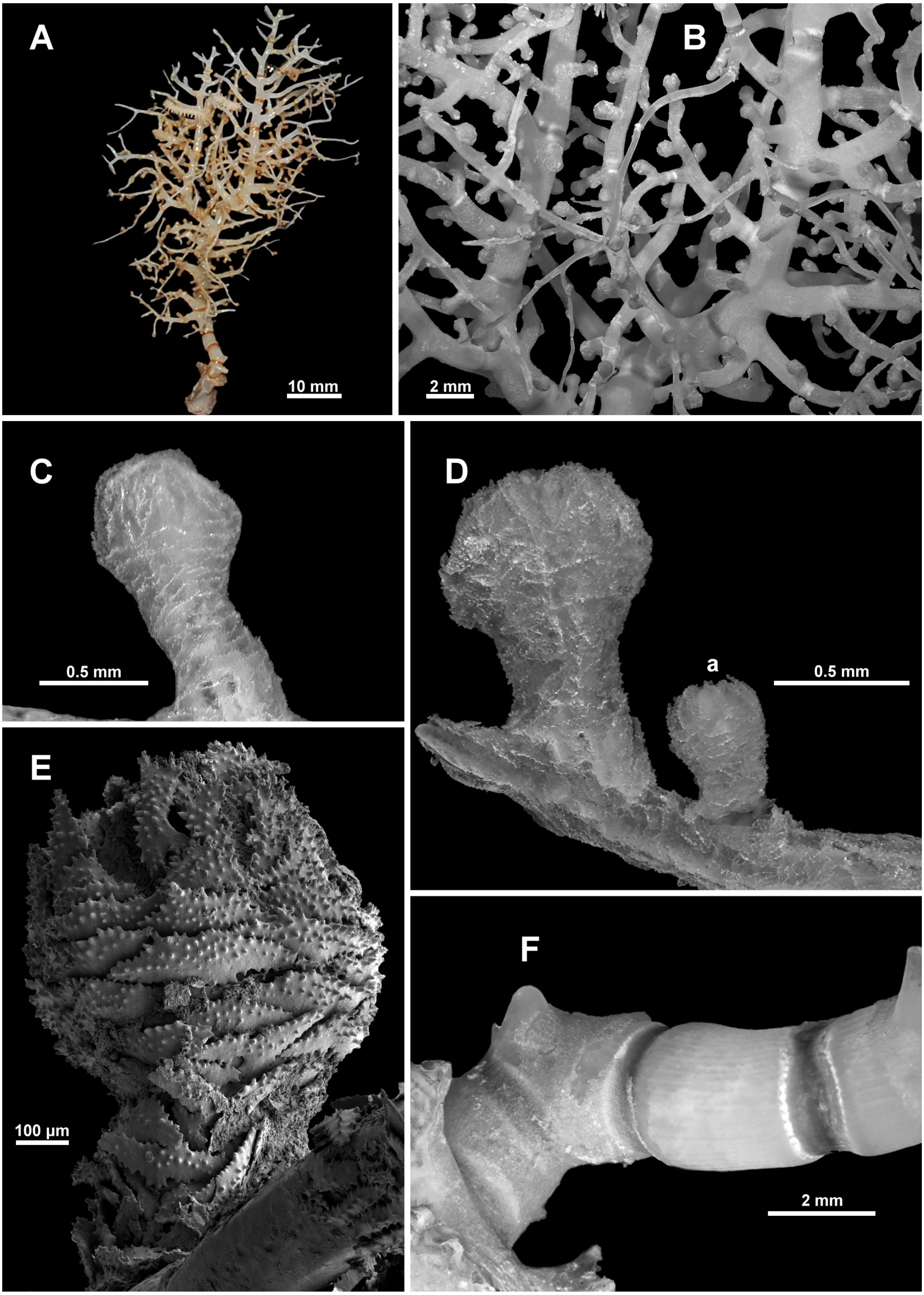

Figure 3.19. *Primnoisis chatham* n. sp., holotype: A. Colony; B. Branching and polyp arrangement; C-E. Polyps (Da. juvenile polyp); F. Proximal axis.

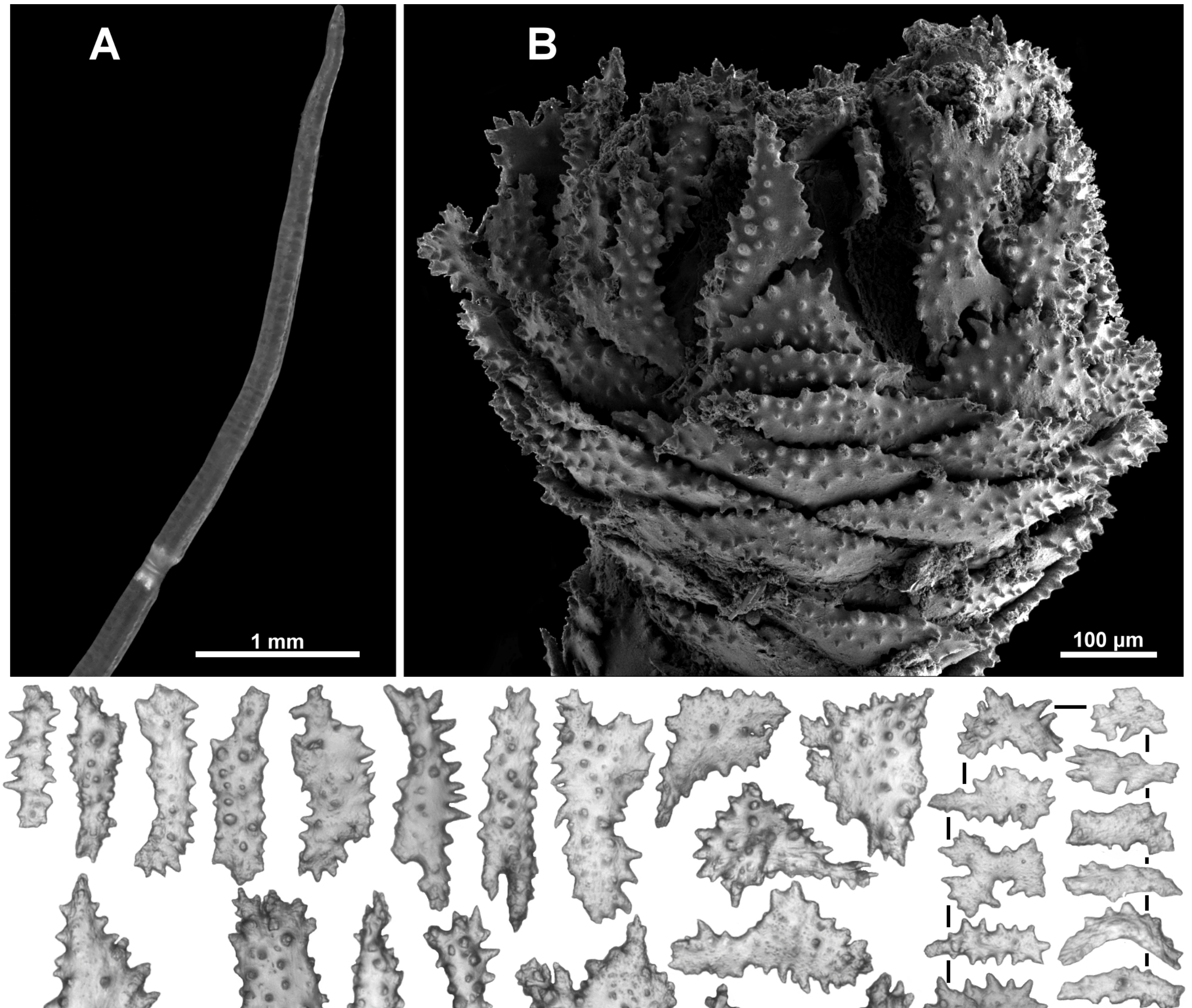

Figure 3.20. *Primnoisis chatham* n. sp., holotype: A. Distal axis; B. Anthopoma in place; C. Anthopoma sclerites; D. Tentacle sclerites.

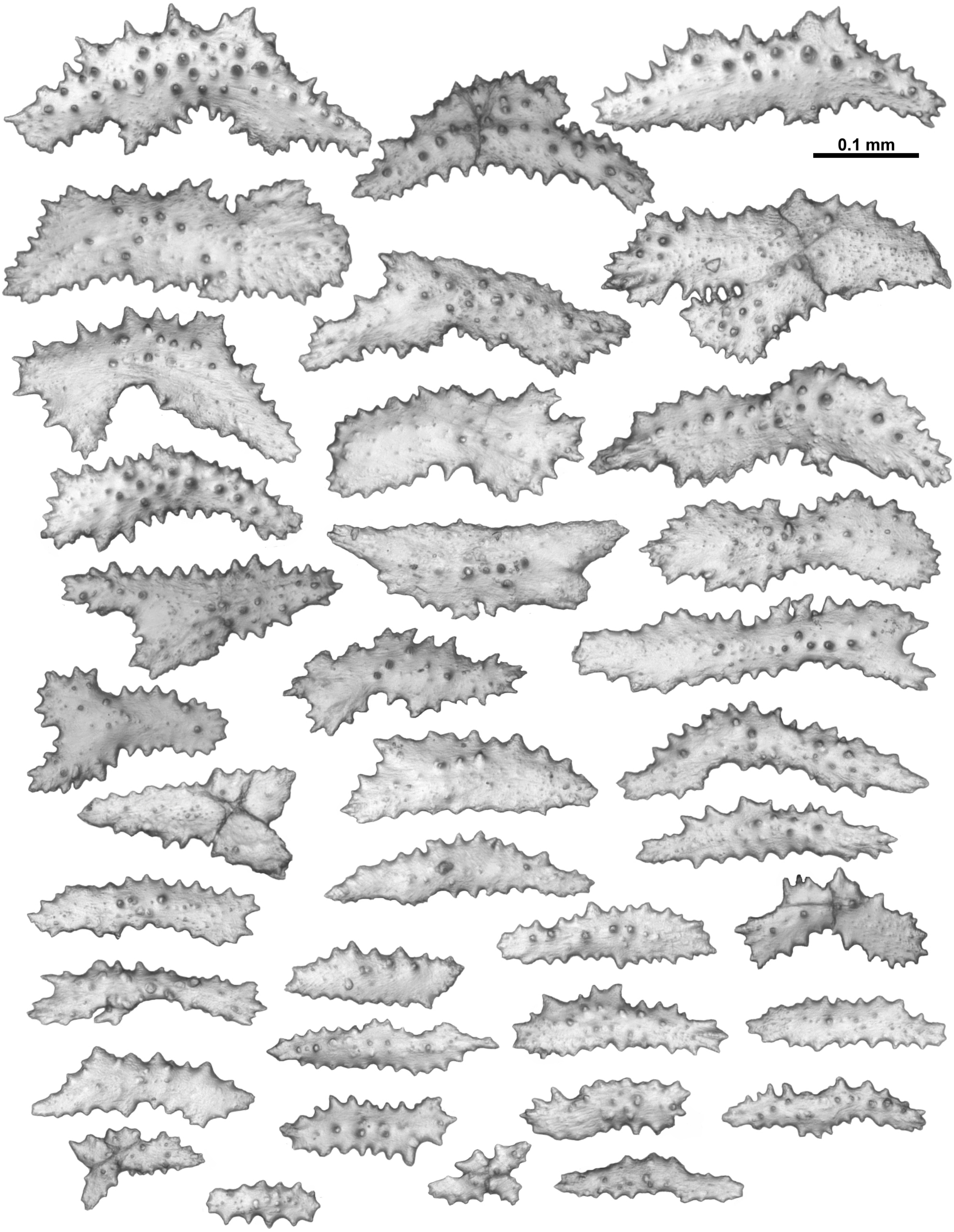

Figure 3.21. *Primnoisis chatham* n. sp., holotype, sclerites: Polyp body.

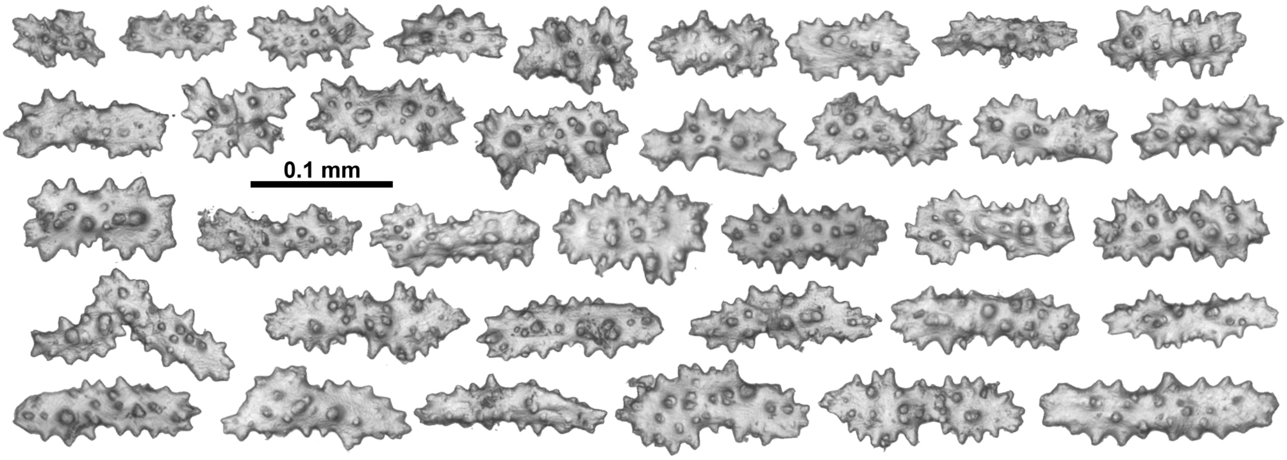

Figure 3.22. *Primnoisis chatham* n. sp., holotype, sclerites: Branch coenenchyme.

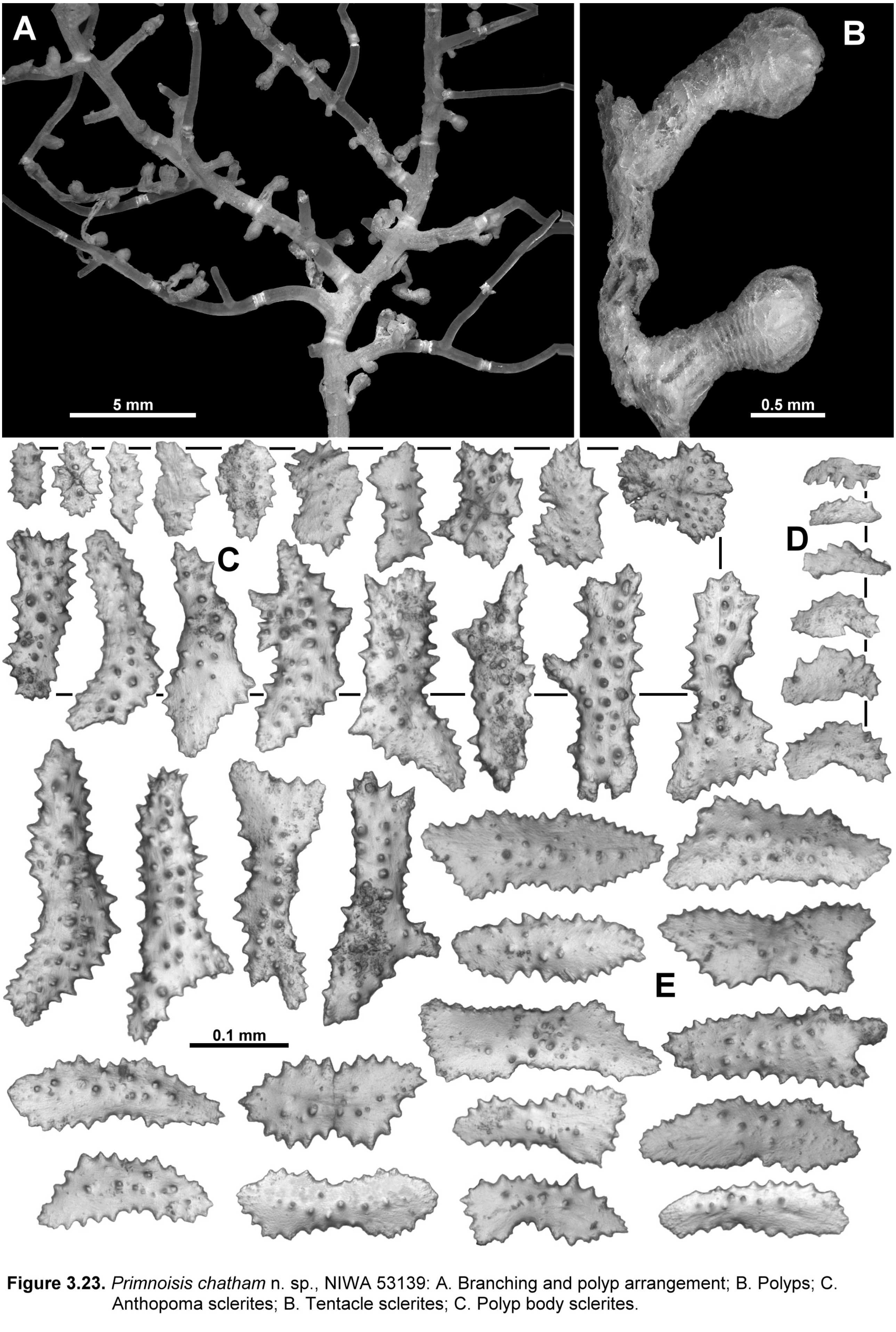

Figure 3.23. *Primnoisis chatham* n. sp., NIWA 53139: A. Branching and polyp arrangement; B. Polyps; C. Anthopoma sclerites; B. Tentacle sclerites; C. Polyp body sclerites.

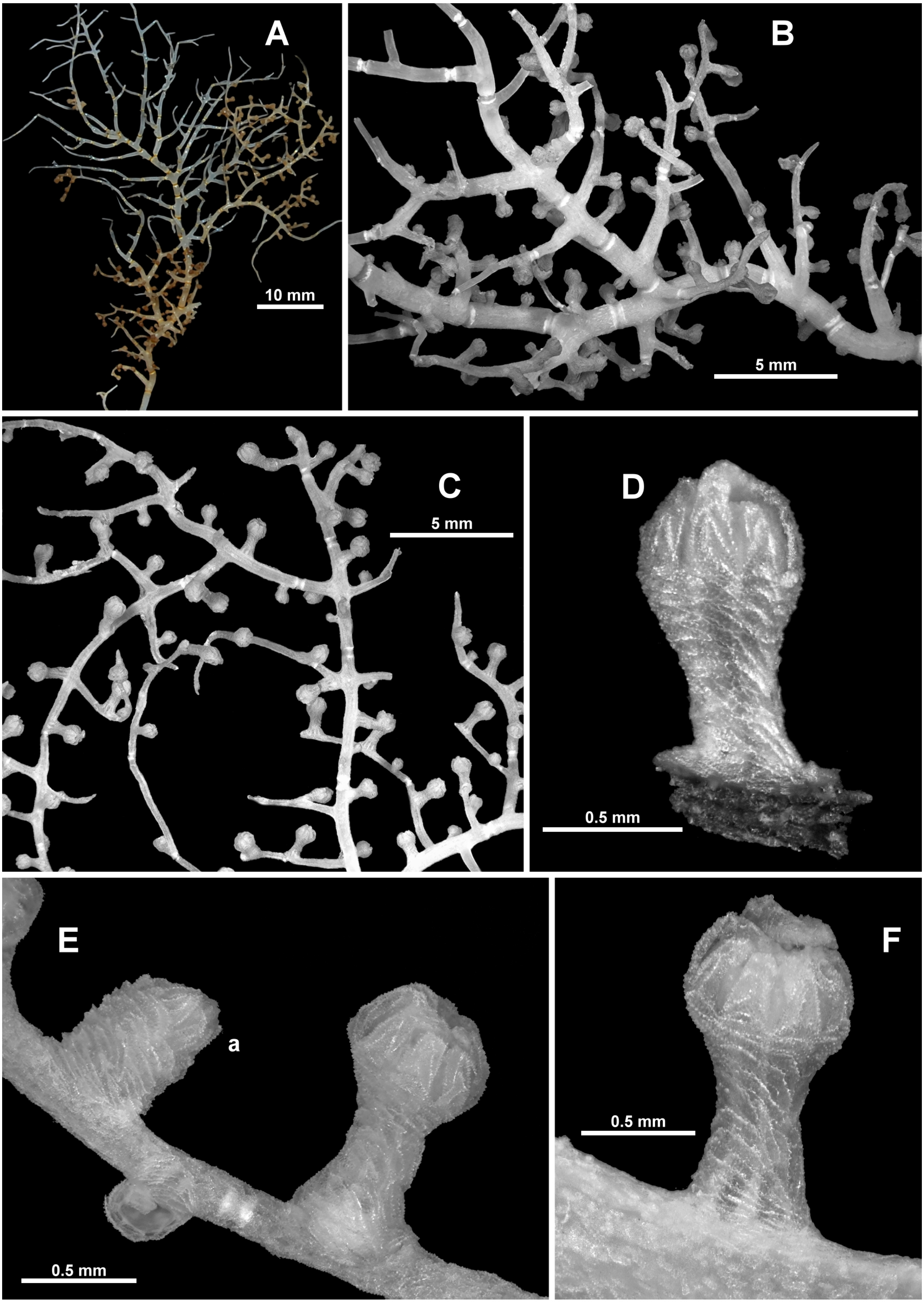

Figure 3.24. *Primnoisis erymna* n. sp., holotype: A. Colony: B-C. Polyp arrangement; D-F. Polyps (Ea. brooding polyp).

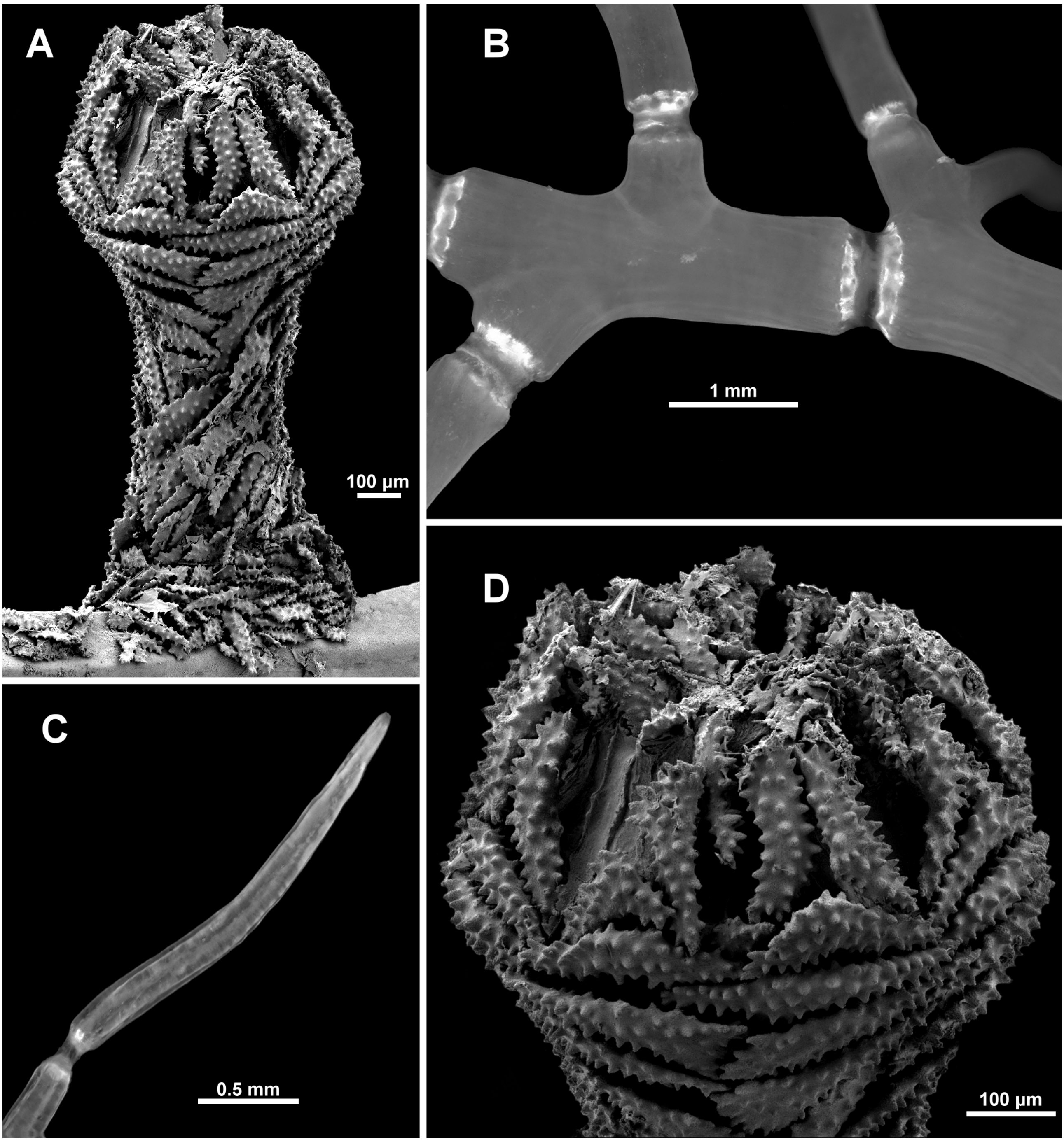

Figure 3.25. *Primnoisis erymna* n. sp., holotype: A. Polyp; B. Proximal axis; C. Twig axis; D. Anthopoma.

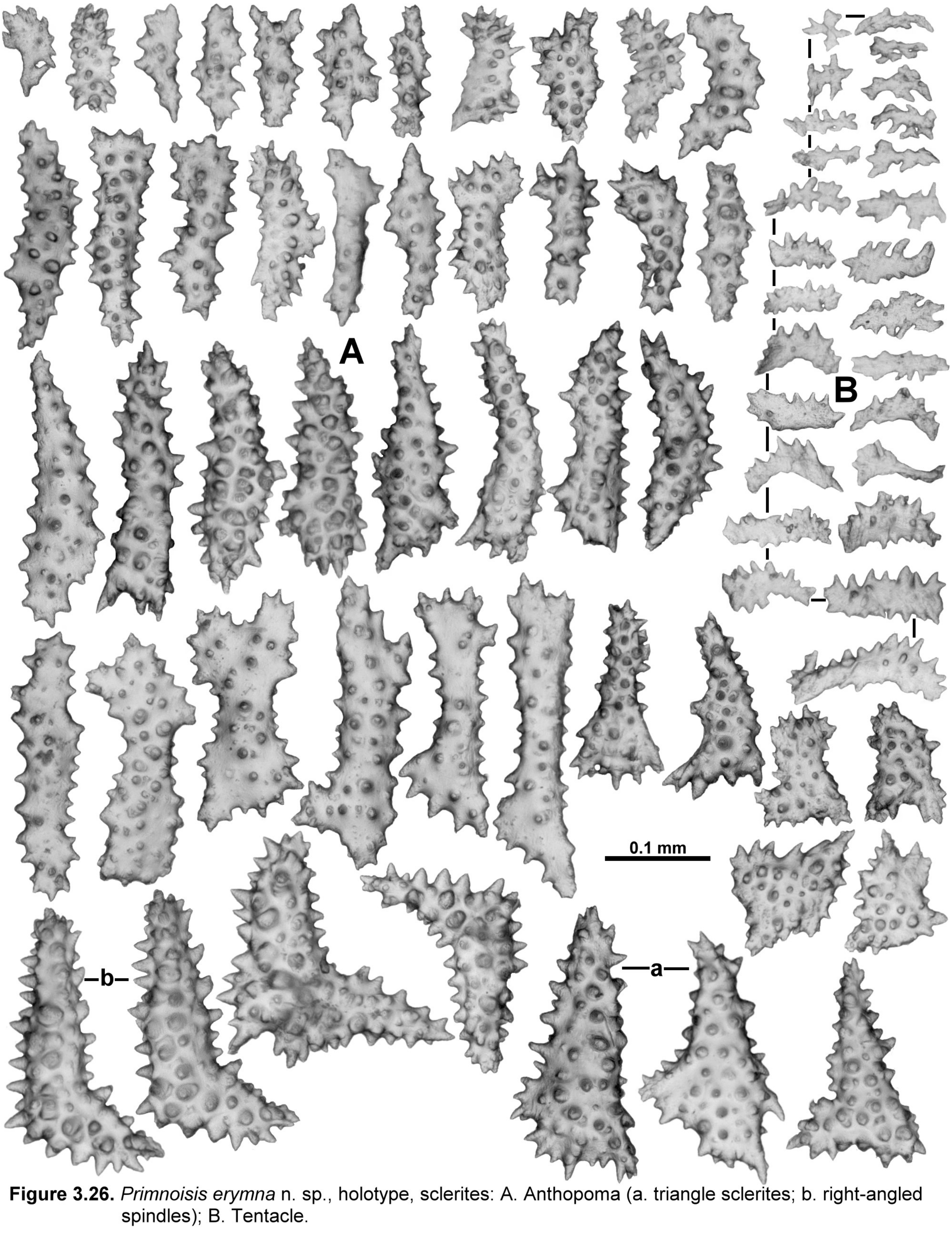

Figure 3.26. *Primnoisis erymna* n. sp., holotype, sclerites: A. Anthopoma (a. triangle sclerites; b. right-angled spindles); B. Tentacle.

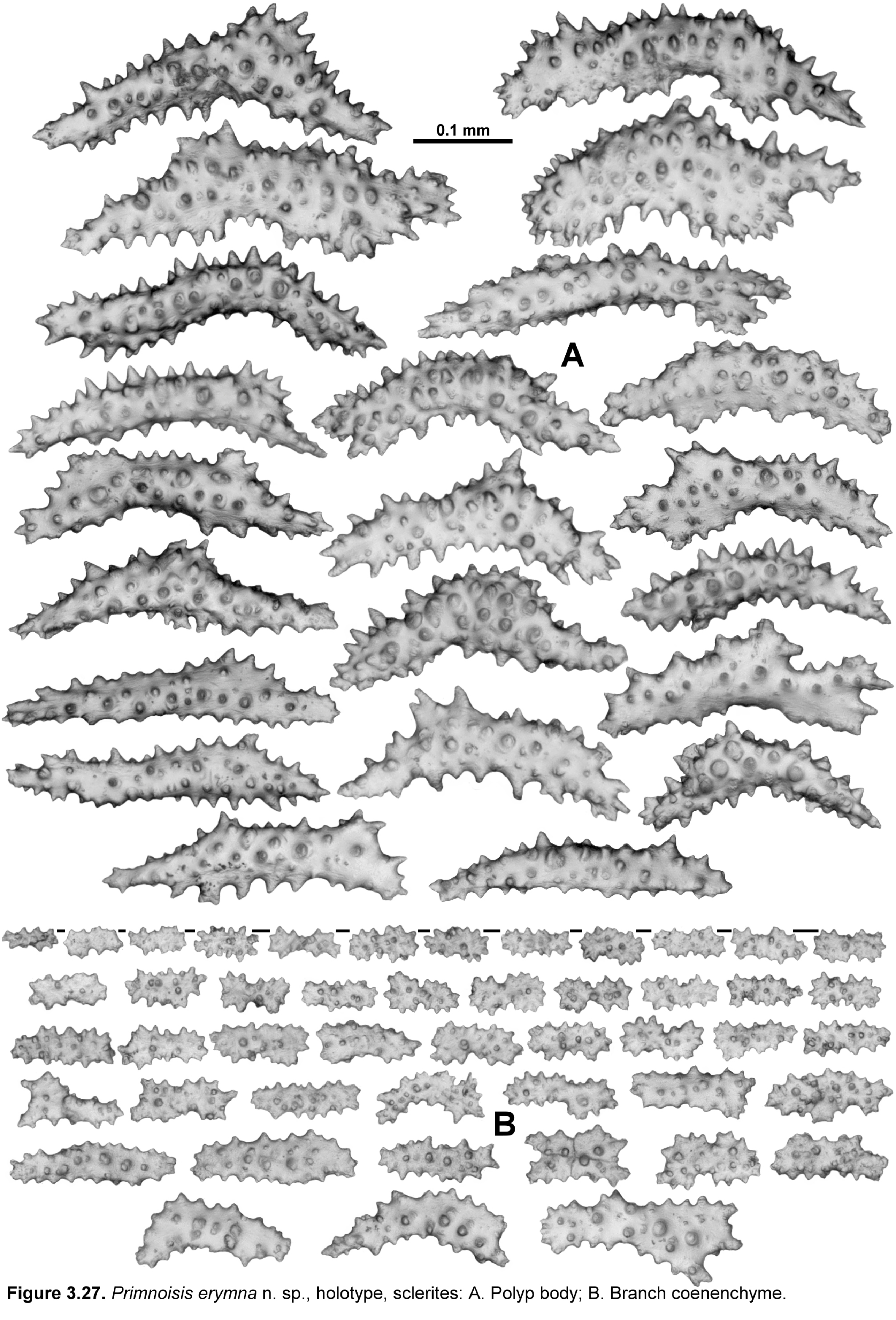

Figure 3.27. *Primnoisis erymna* n. sp., holotype, sclerites: A. Polyp body; B. Branch coenenchyme.

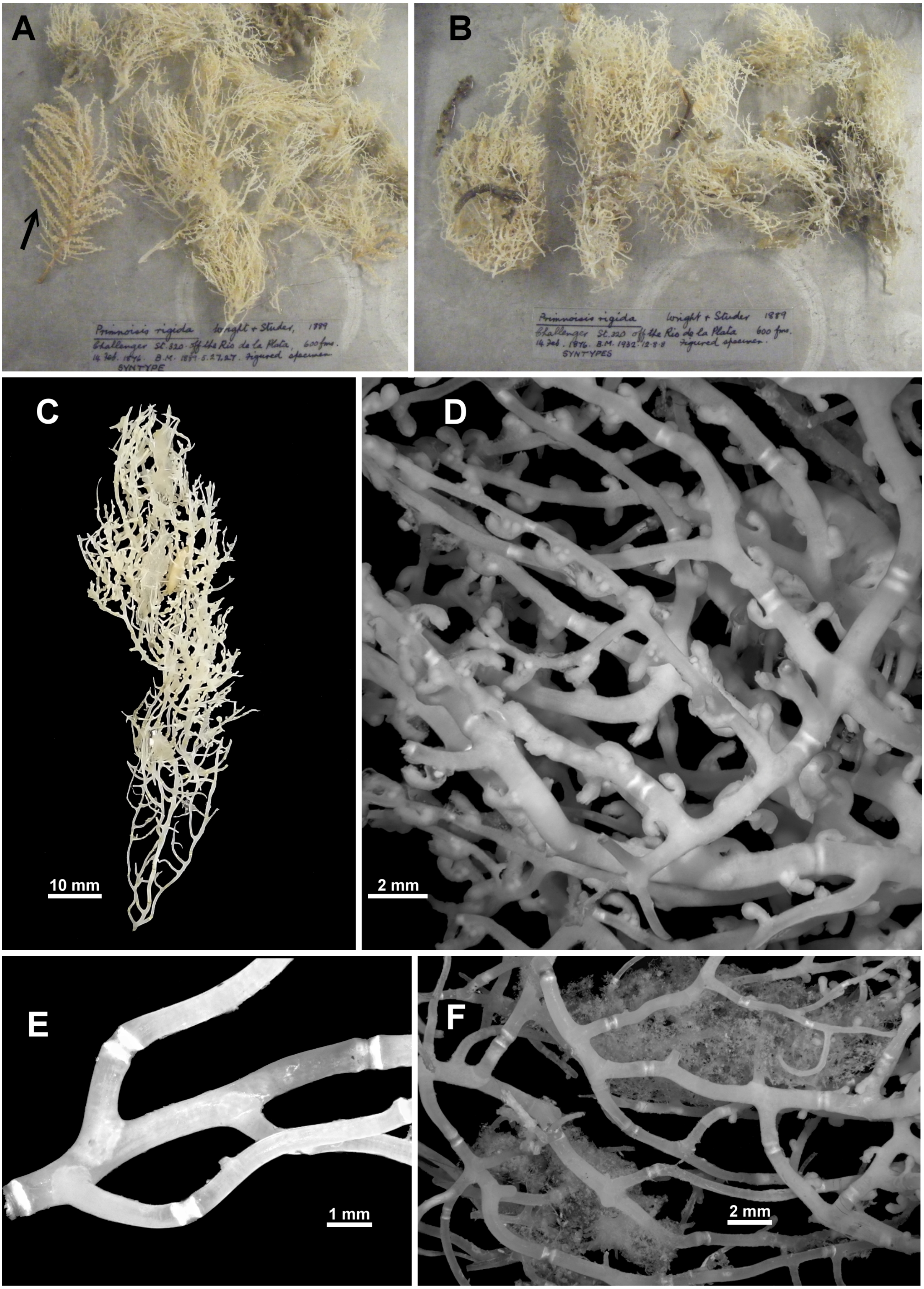

Figure 3.28. *Primnoisis rigida* Wright & Studer, 1889; A. Syntype NHMUK 1889.5.27.27 (arrow to Primnoidae colony). B-F. Syntype NHMUK1932.12.8.8, (B). Colony; (C). Fragment examined; (D). Proximal branches; (E). Curved junctions; (F). Distal branches.

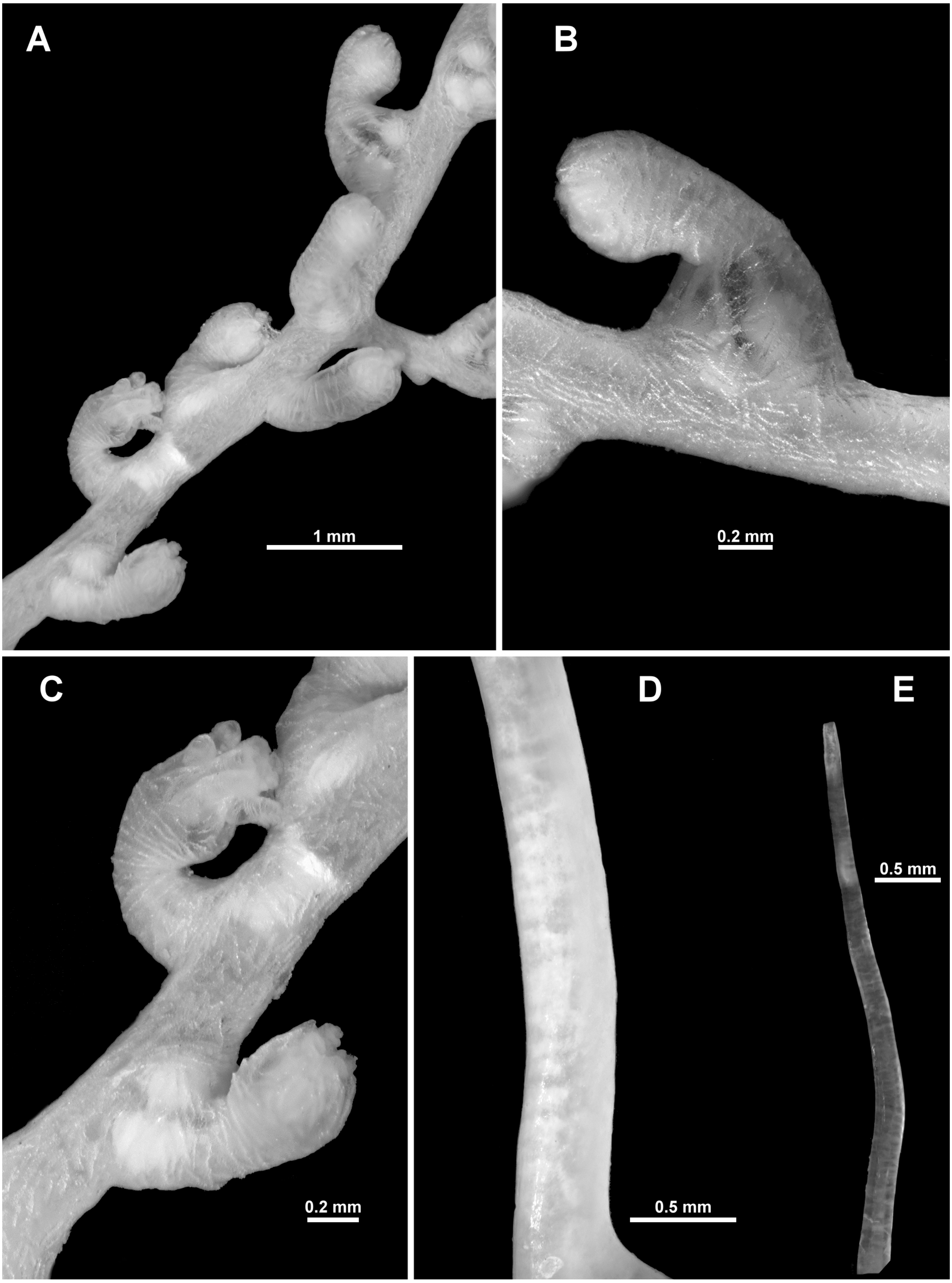

Figure 3.29. *Primnoisis rigida* Wright & Studer, 1889; syntype: A. Portion of a branch; B. Rounded polyp with eggs; C. Enlargement of A. showing a polyp with tentacles partly extended and a polyp with eggs; D. Proximal axis; E. Twig axis.

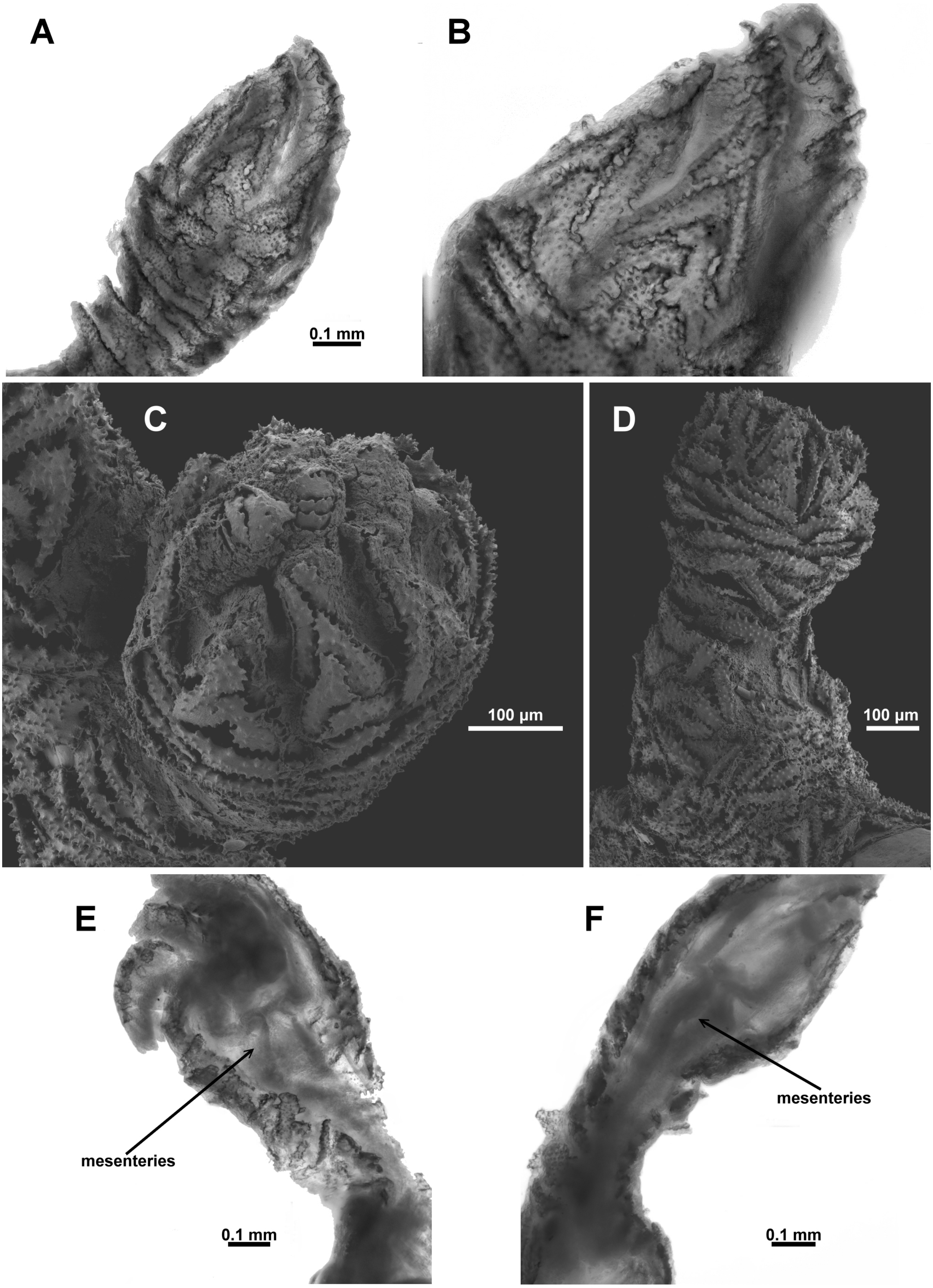

Figure 3.30. *Primnoisis rigida* Wright & Studer, 1889; syntype: A. Polyp head; B-C. Close-up of A. showing the anthopoma in place; D. Polyp; E-F. Longitudinal sections of polyp with mesenteries indicated.

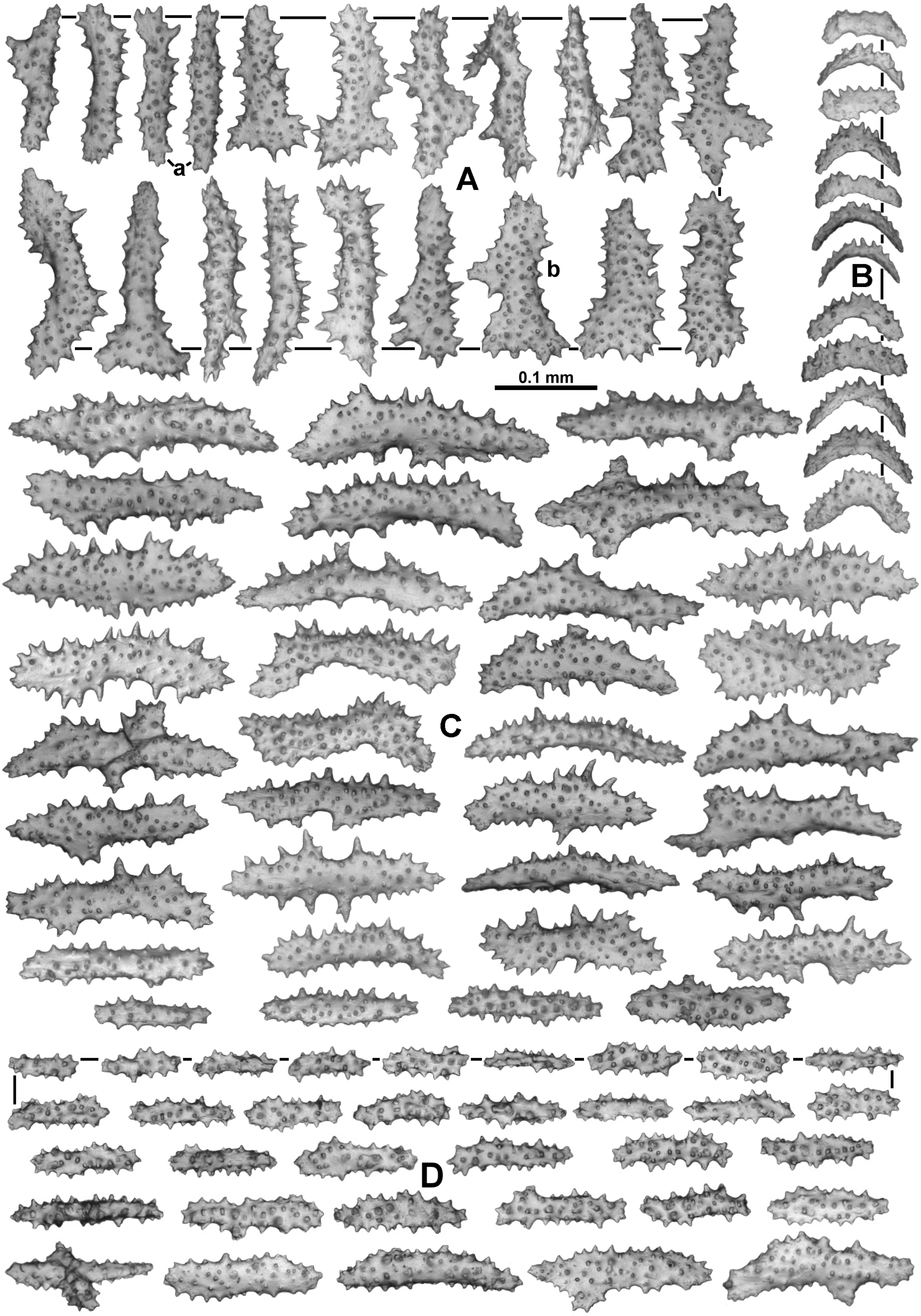

Figure 3.31. *Primnoisis rigida* Wright & Studer, 1889; syntype, sclerites: A. Anthopoma (a.narrow, tuberculate rods; b. porximal flattened sclerite); B. Tentacle: C. Polyp

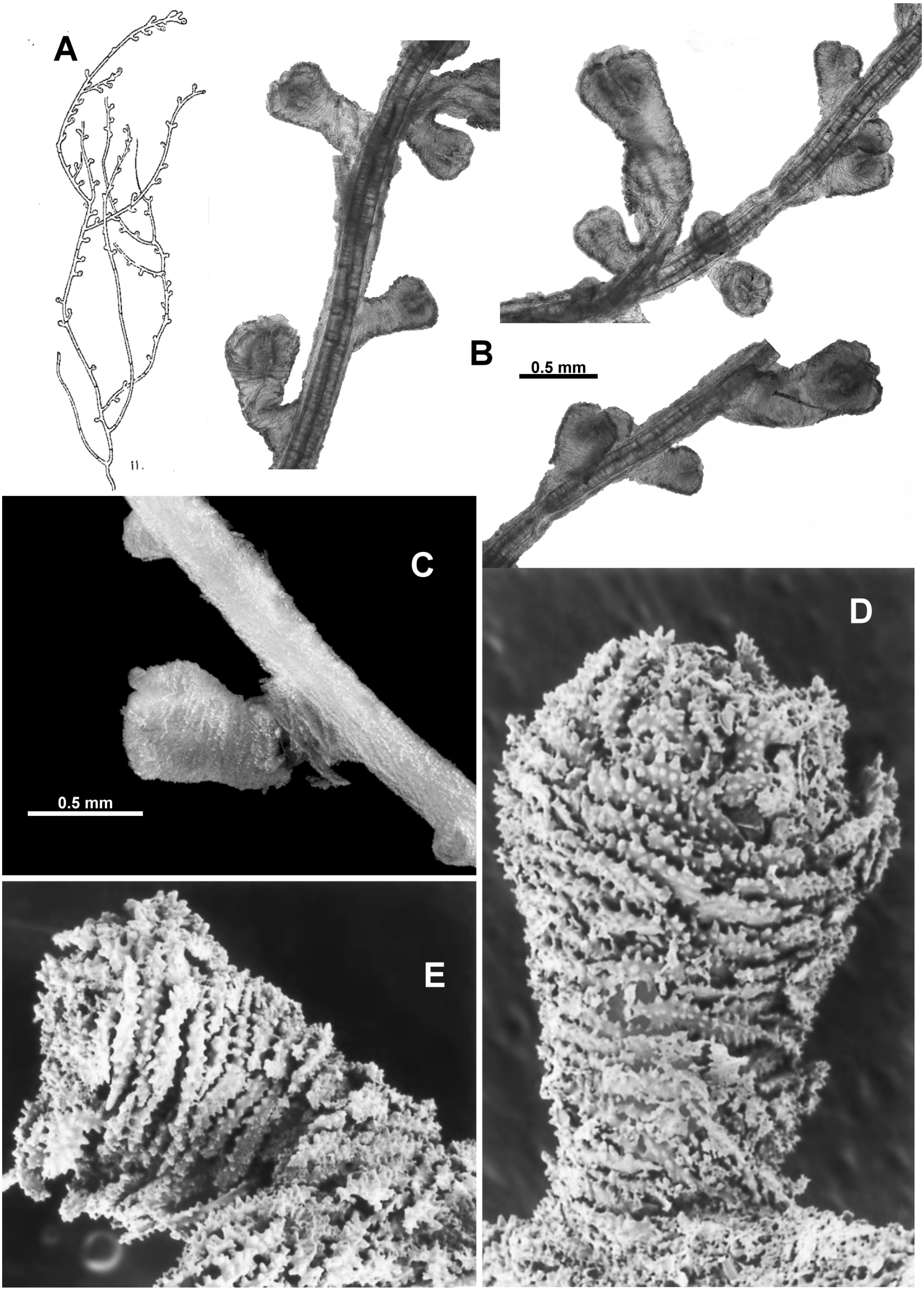

Figure 3.32. *Primnoisis delicatula* (Hickson, 1907), syntype: A. Colony figure from Hickson 1907, Pl. II Fig. 11; B. Branch fragments on slide NHMUK 1961.3.9.152; C-E. Polyps. (C. Courtesy of Dr P. Alderslade, D-E. from Alderslade 1988, Fig. 202C and 202B respectively).

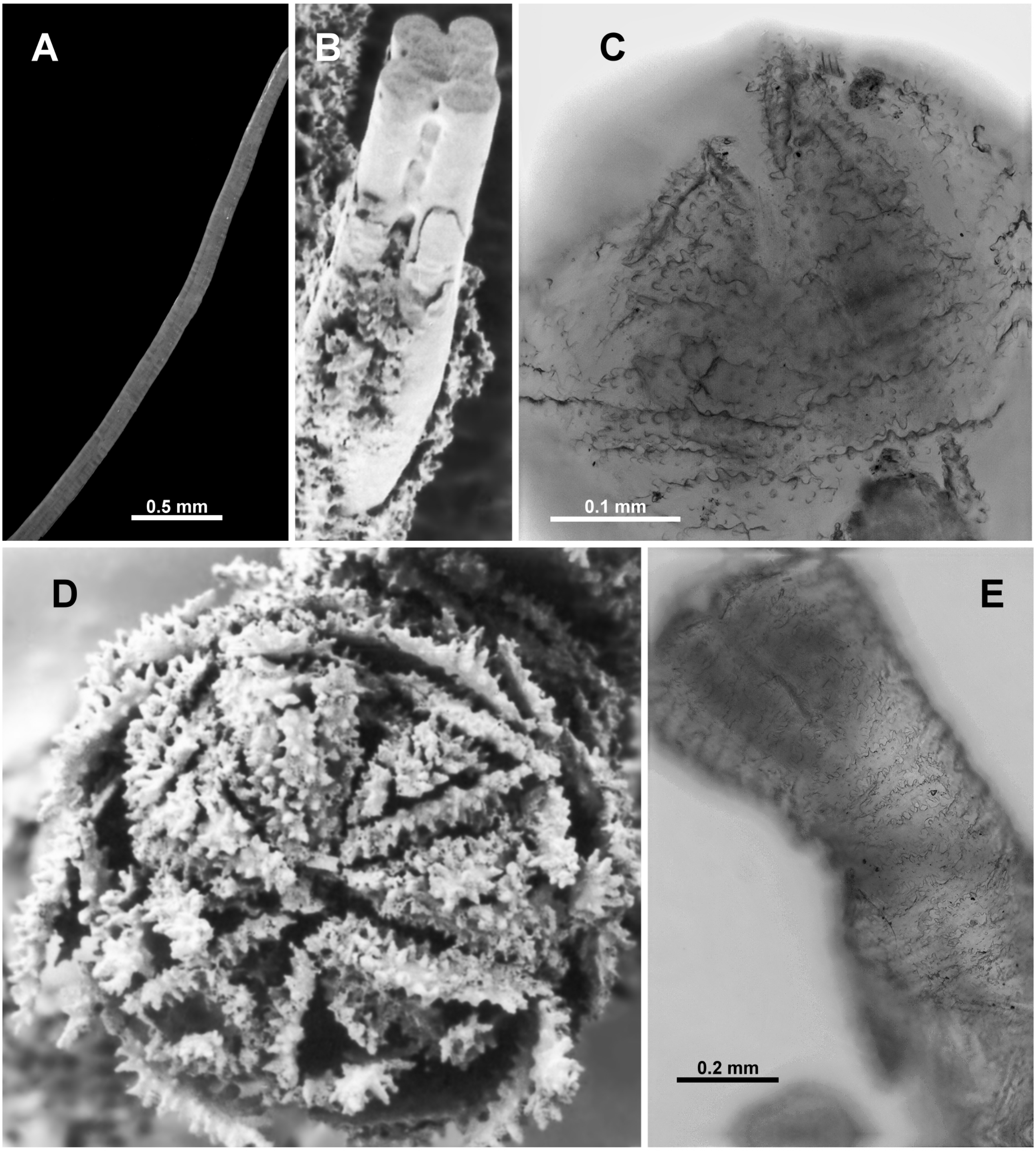

Figure 3.33. *Primnoisis delicatula* (Hickson, 1907), syntype: A. Distal twig; B. Axial internode; C-D. Anthopoma; E. Polyp body sclerites. (B., D. from Alderslade 1998, Fig. 202E and 202A respectively).

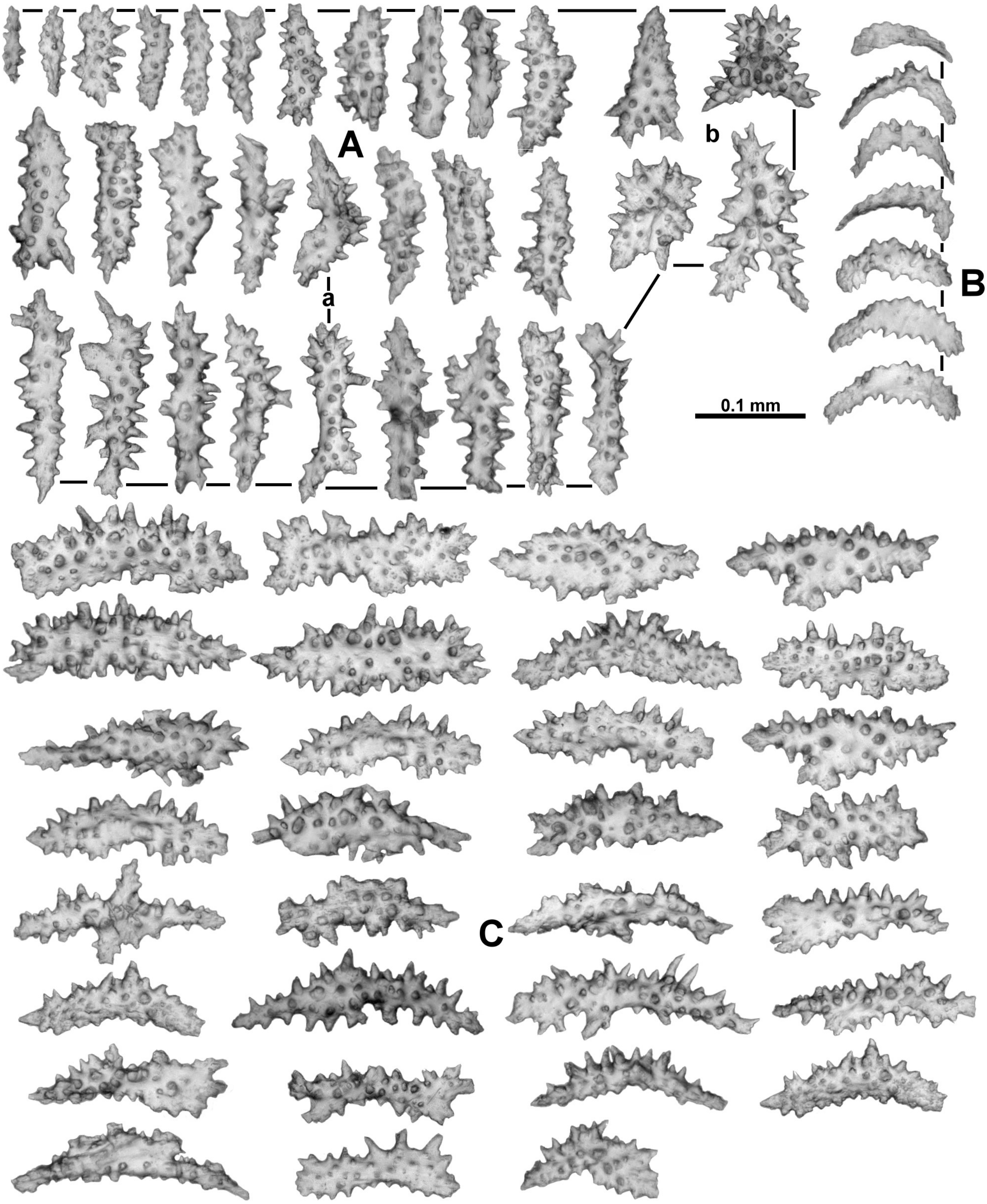

Figure 3.34. *Primnoisis delicatula* (Hickson, 1907), syntype, sclerites: A. Anthopoma (a. irregularly shaped sclerites; b. irregular transitional sclerites); B. Tentacles; C. Polyp body.

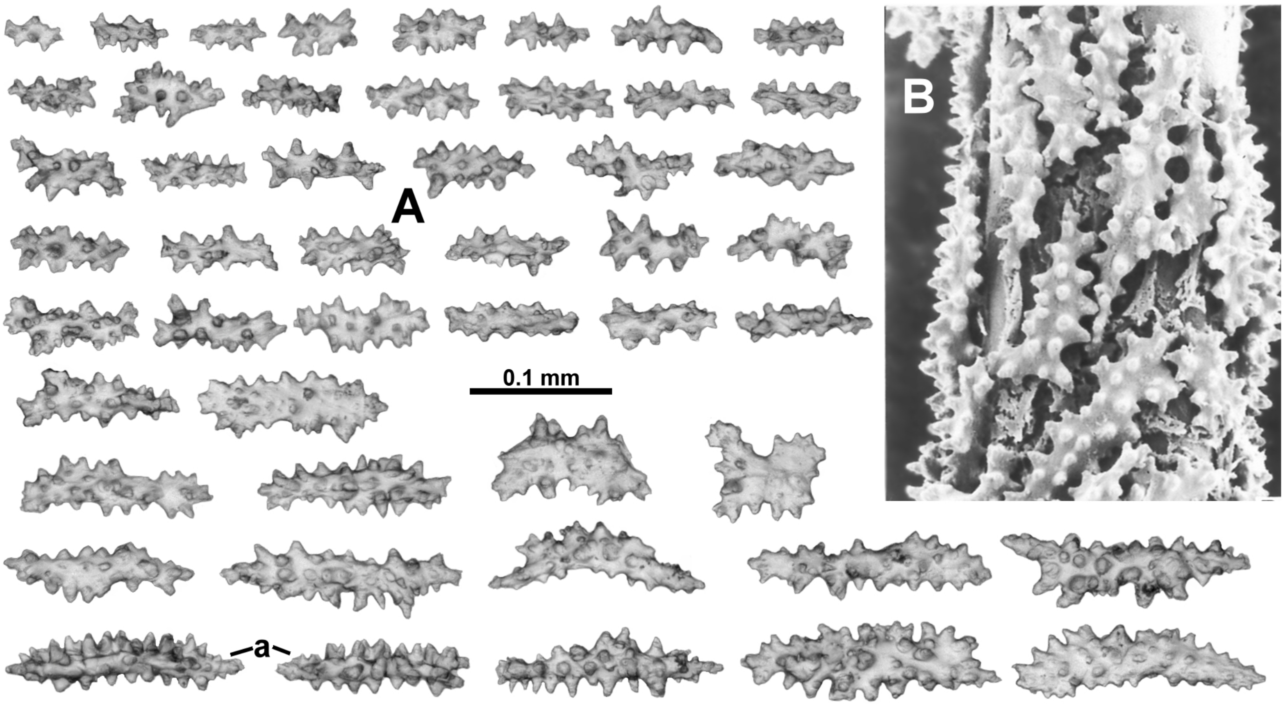

Figure 3.35. *Primnoisis delicatula* (Hickson, 1907), syntype: A. Twig coenenchyme sclerites (a. rounded, tuberculate sclerites); B. Coenenchyme (B. From Alderslade 1998, Fig. 202D).

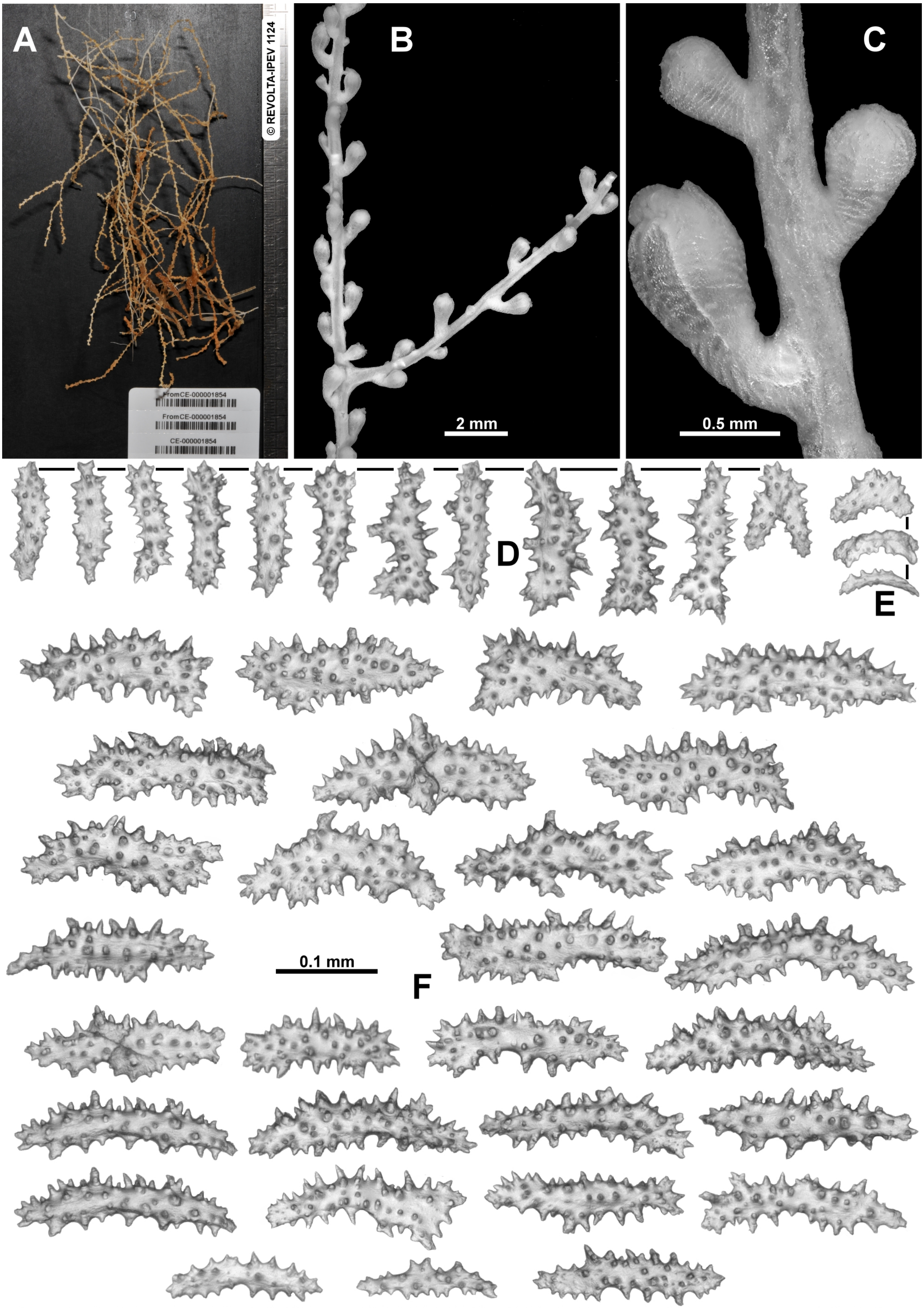

Figure 3.36. *Primnoisis delicatula* Hickson, 1907, MNHN CE-1854; A. Colony; B. Polyp arrangement; C. Polyps; D. Anthopoma sclerites; E. Tentacle sclerites; F. Polyp body sclerites. (A. Courtesy of MNHN staff).

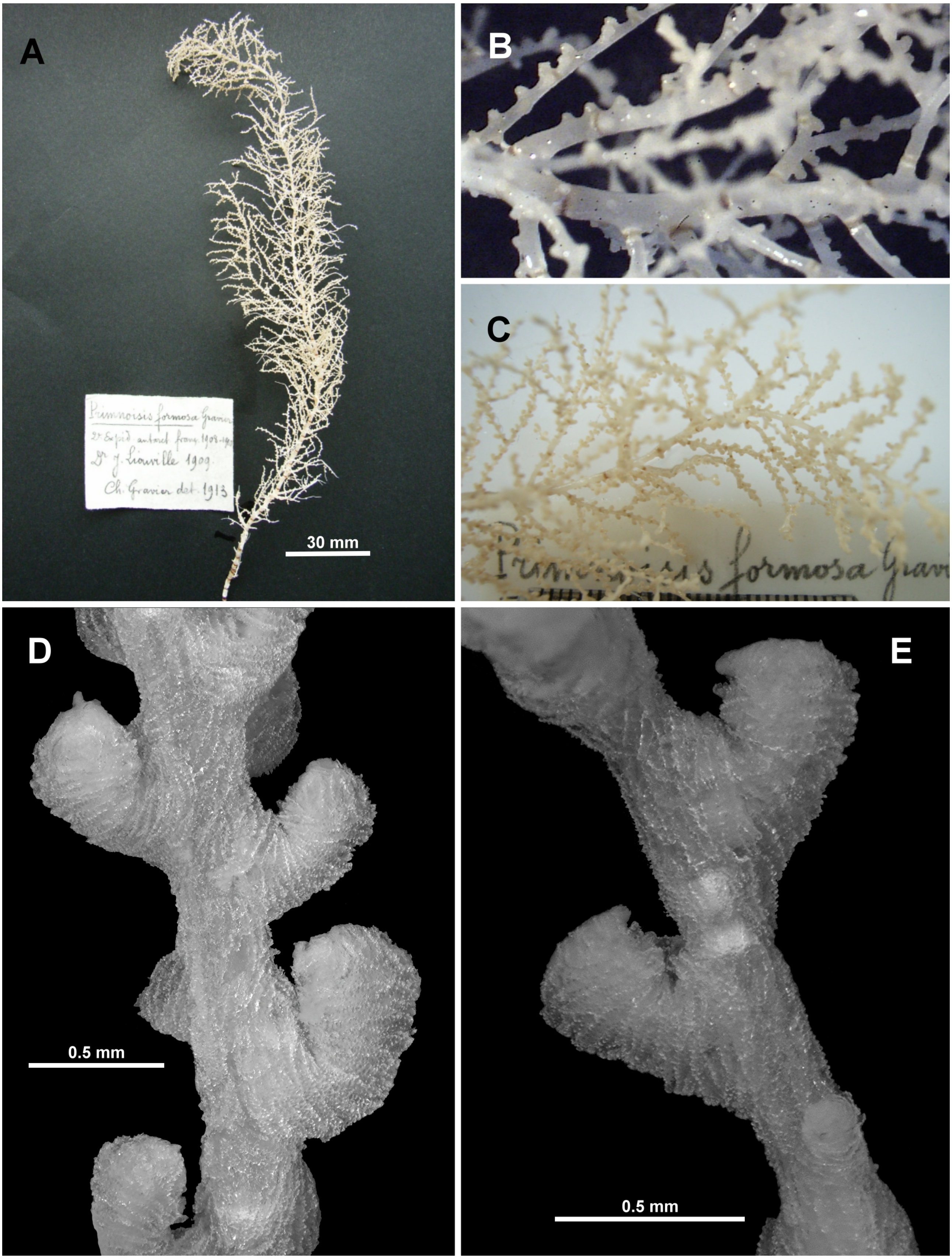

Figure 3.37. *Primnoisis formosa* Gravier, 1913, holotype: A. Colony; B-C. Branching; D-E. Polyps.

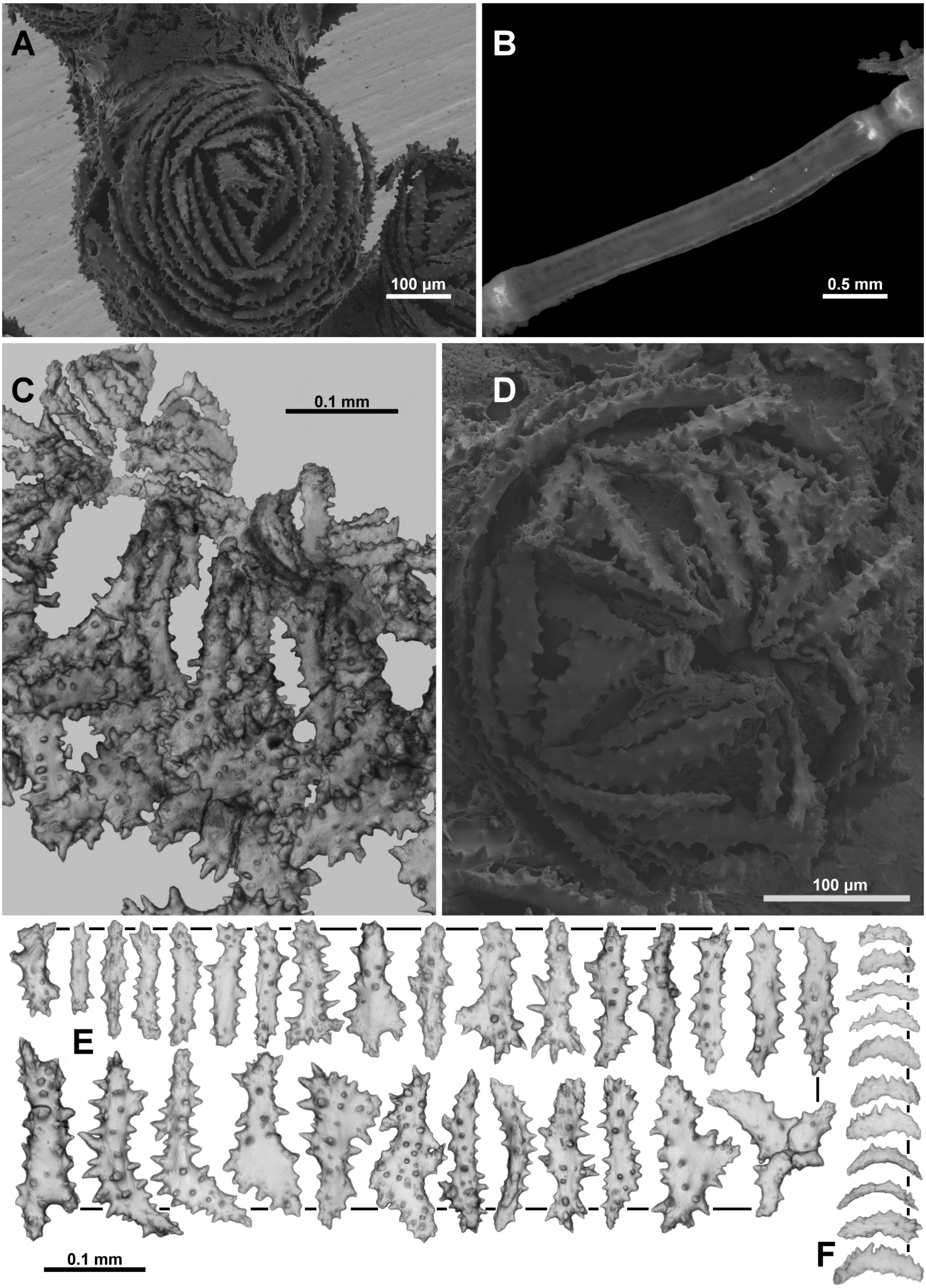

Figure 3.38. *Primnoisis formosa* Gravier, 1913: A. MNHN CE-0629, brooding polyp. B-C, E-F. Holotype: (B).Twig axis; (C). Anthopoma sclerites in situ; (E). Anthopoma sclerites; (F). Tentacle sclerites; D. MNHN CE-0629, anthopoma in situ.

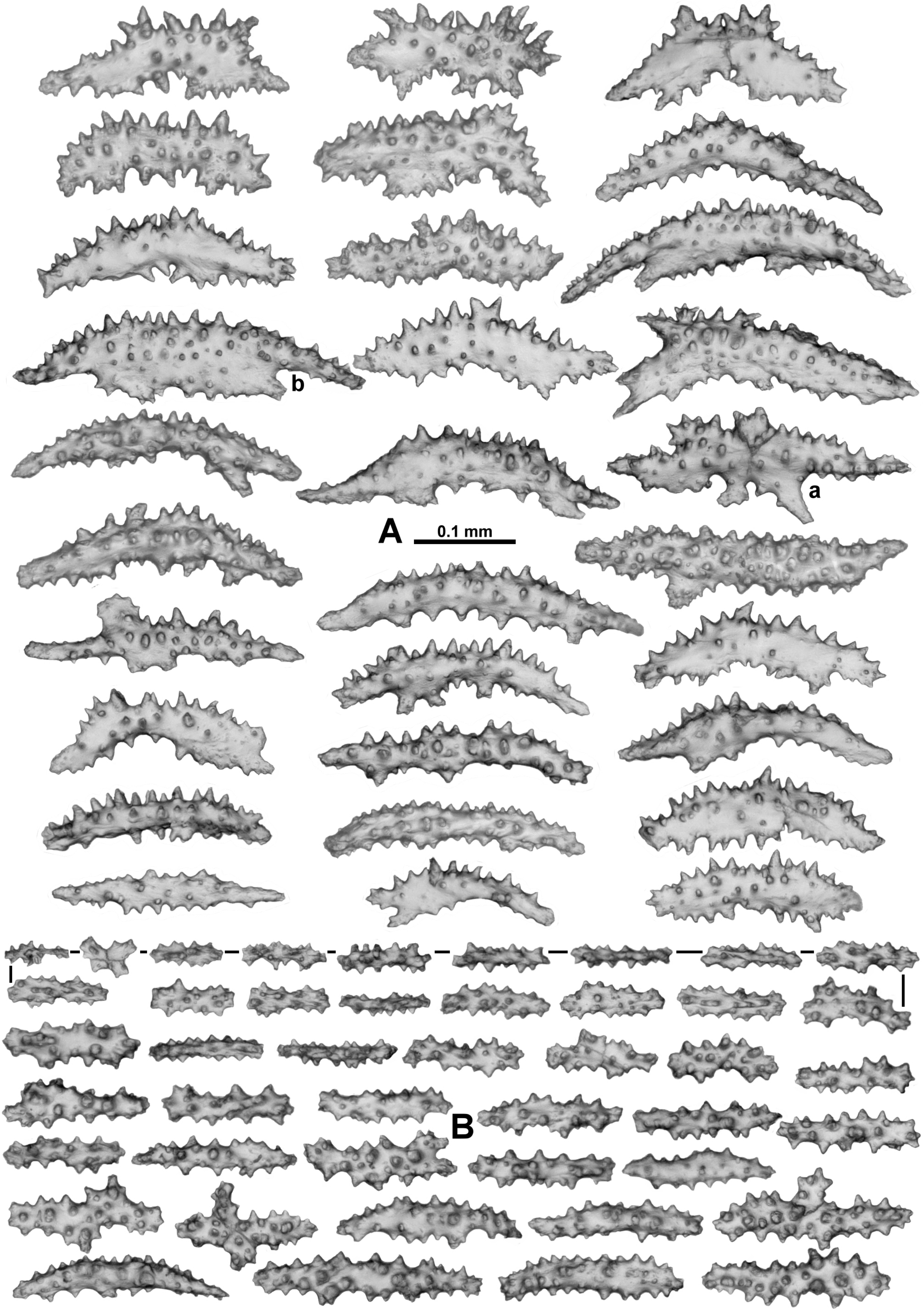

Figure 3.39. *Primnoisis formosa* Gravier, 1913, holotype, sclerites: A. Polyp body (a, b. sclerites with root-like extensions); B. Branch coenenchyme.

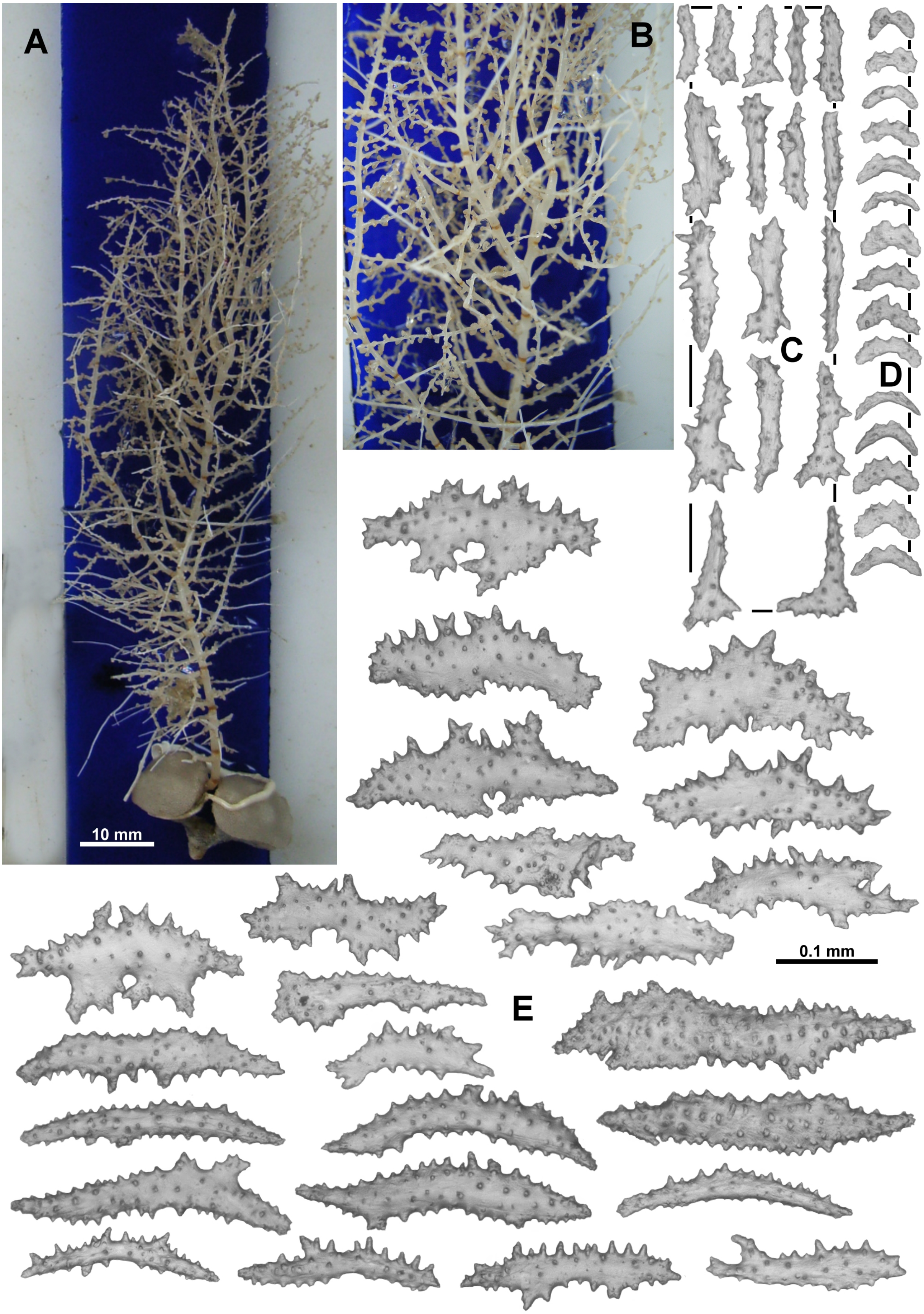

Figure 3.40. ?*Primnoisis formosa* Gravier, 1913, paratype MNHN OCT223: A-B. Colony; C. Anthopoma sclerites; D. Tentacle sclerites; E. Polyp body sclerites.

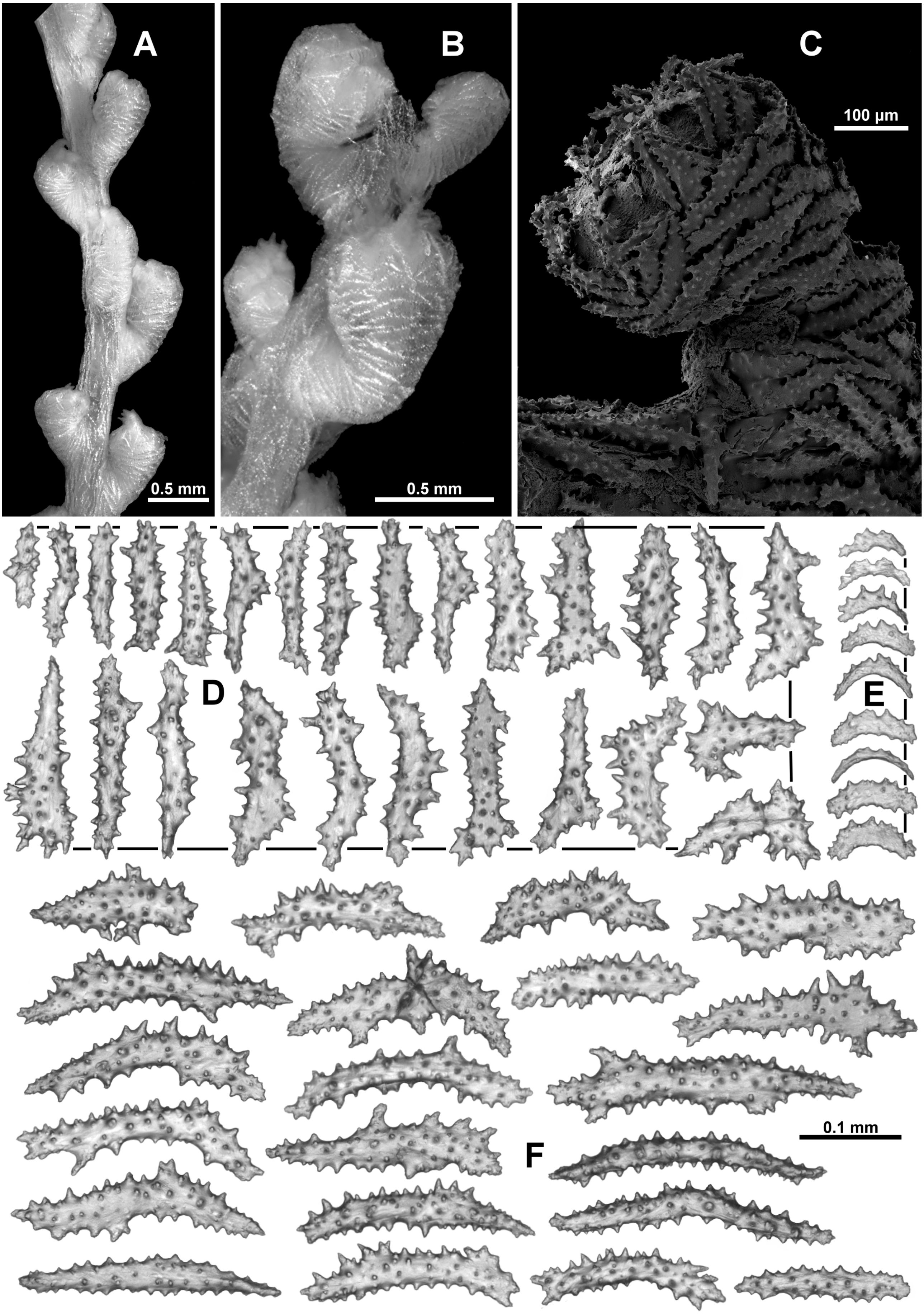

Figure 3.41. *Primnoisis formosa* Gravier, 1913, MNHN CE-1535: A-C. Polyps; D. Anthopoma sclerites; E. Tentacle sclerites; F. Polyp body sclerites.

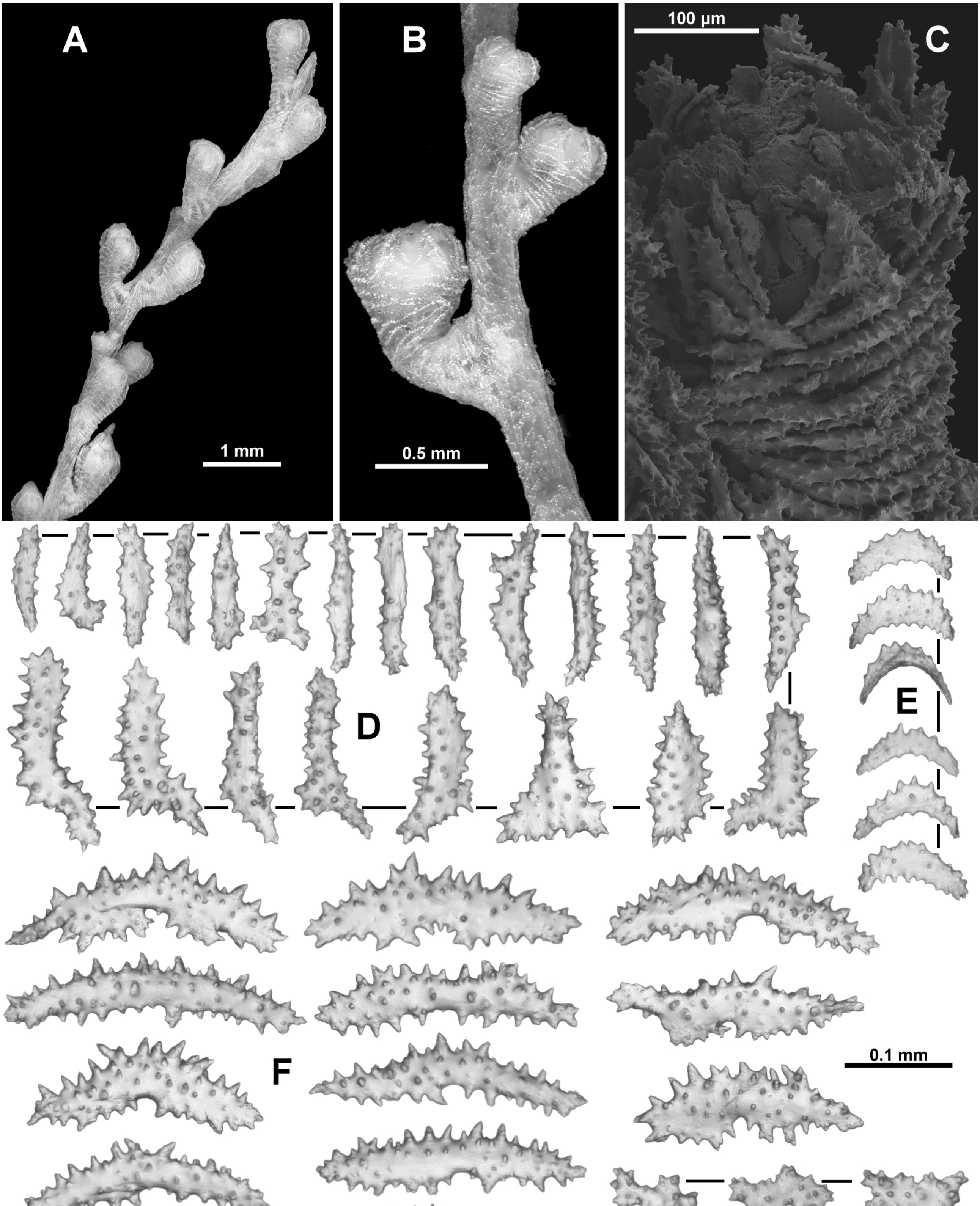

Figure 3.42. *Primnoisis formosa* Gravier, 1913, TMAG K4297: A-C. Polyps; D. Anthopoma sclerites; E. Tentacle sclerites; F. Polyp body sclerites; G. Branch coenenchyme sclerites.

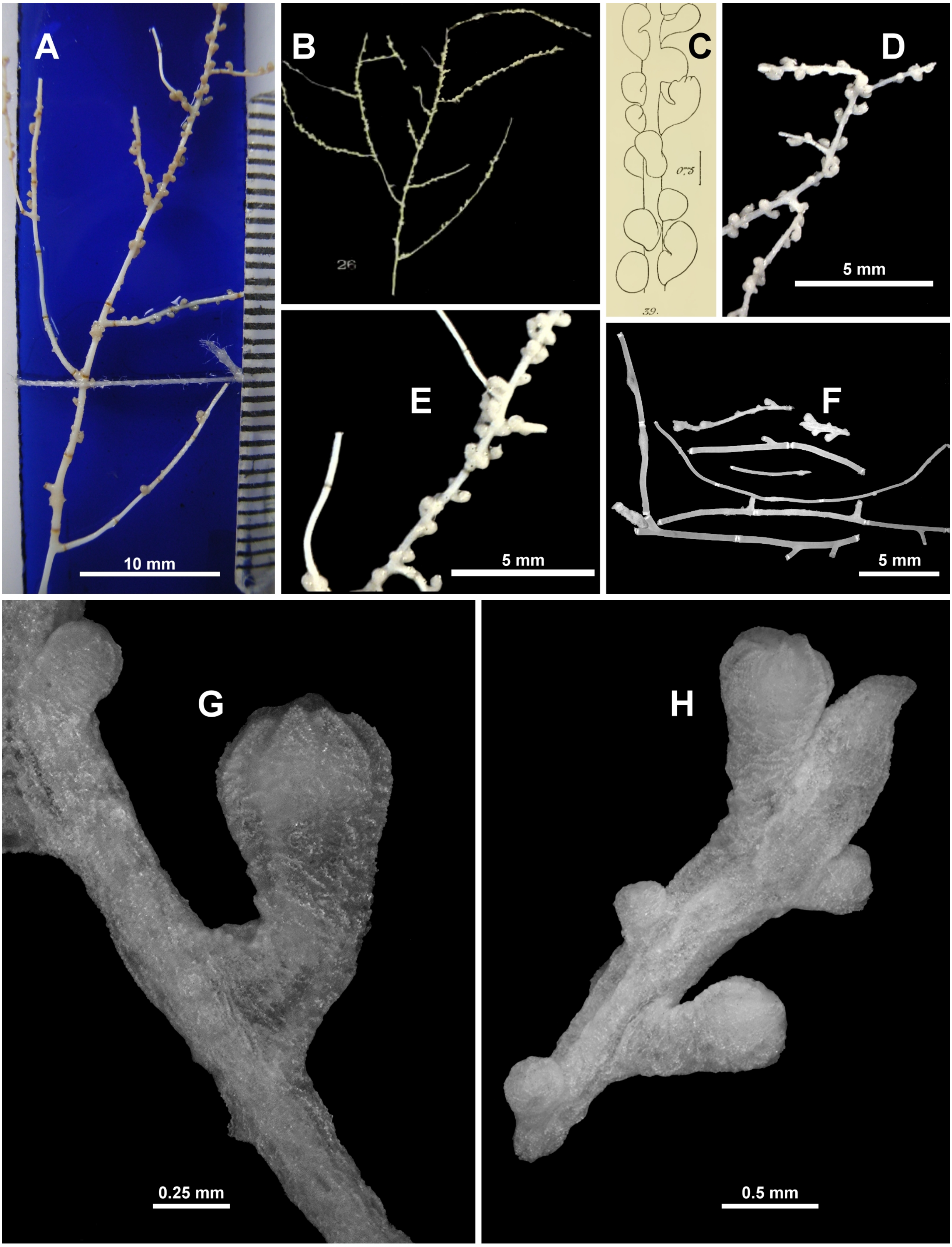

Figure 3.43. *Primnoisis gracilis* (Gravier, 1913): A-E. Holotype: (A). Colony; (B). Gravier's colony figure; (C-E). Polyps on distal twigs. F-H. Paratype, MNHN OCT- 214: (F). Colony fragments; (G-H). Polyps. (B., C. From Gravier 1914: Pl. VI, Fig.26 & Textfig. 39 respectively).

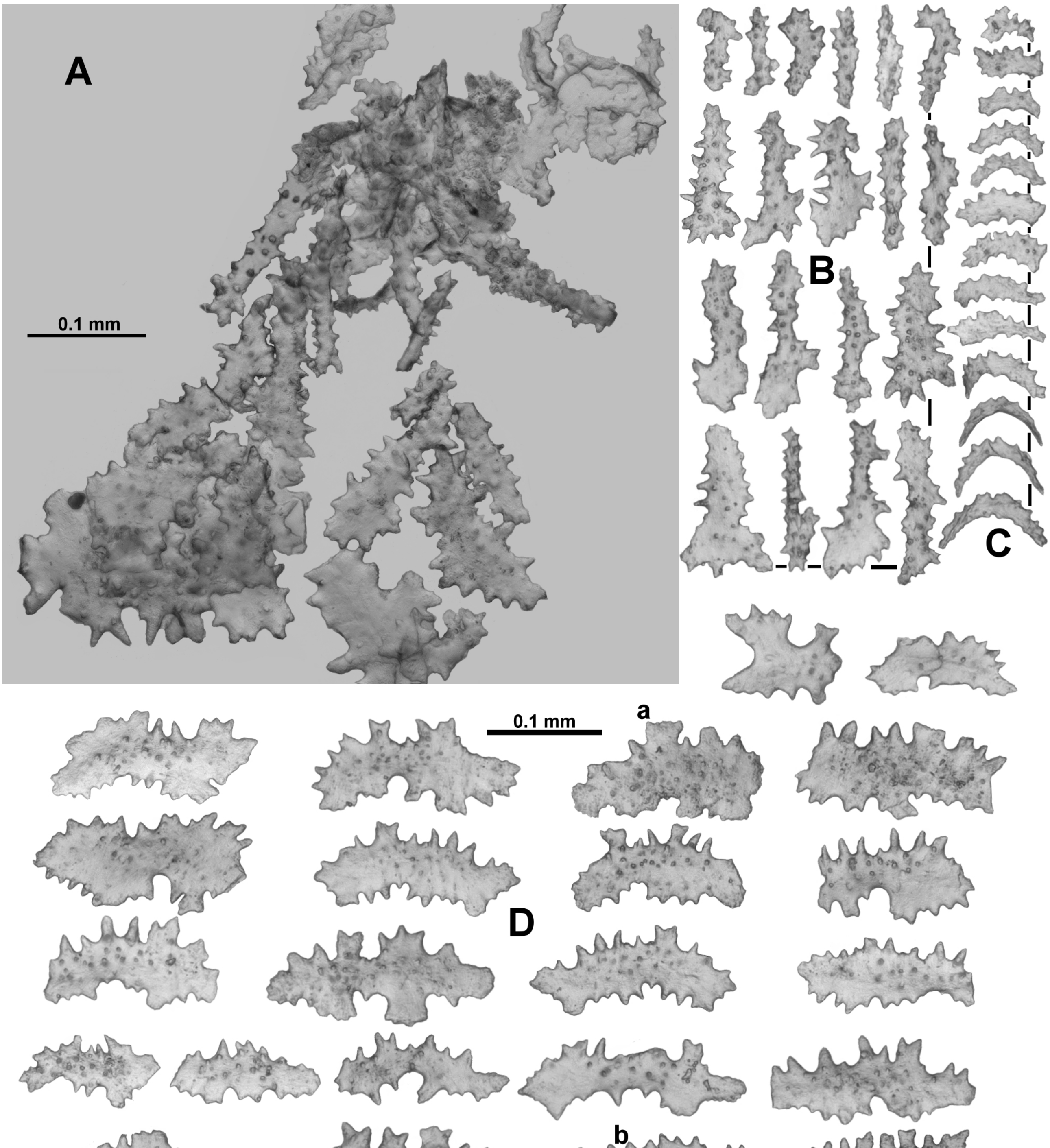

Figure 3.44. *Primnoisis gracilis* (Gravier, 1913), holotype: A. Anthopoma sclerites in situ; B. Anthopoma sclerites C. Tentacle sclerites; D. Polyp body sclerites (a. sclerite with blunt peaks; b. sclerite from near the polyp base).

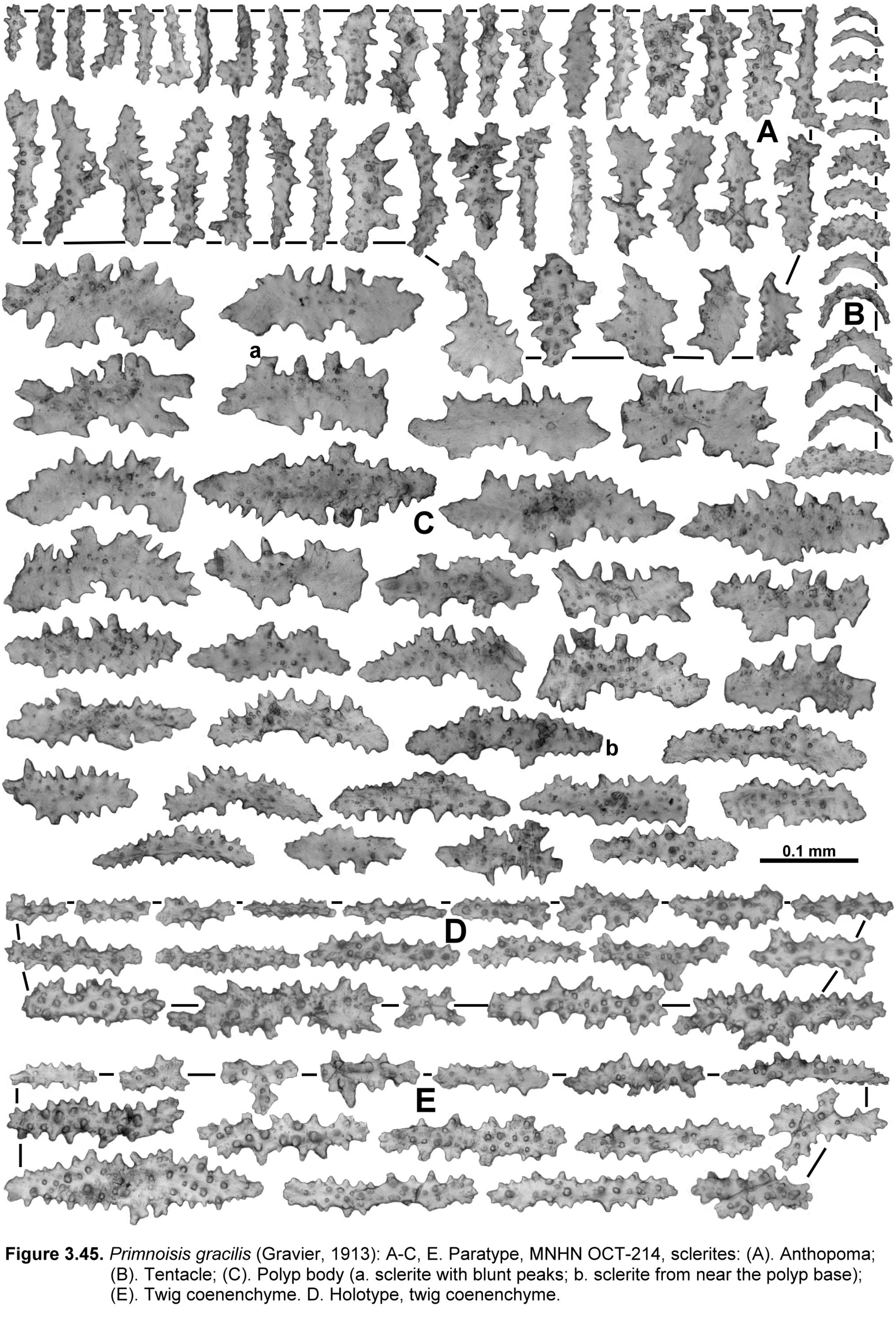

Figure 3.45. *Primnoisis gracilis* (Gravier, 1913): A-C, E. Paratype, MNHN OCT-214, sclerites: (A). Anthopoma; (B). Tentacle; (C). Polyp body (a. sclerite with blunt peaks; b. sclerite from near the polyp base); (E). Twig coenenchyme. D. Holotype, twig coenenchyme.

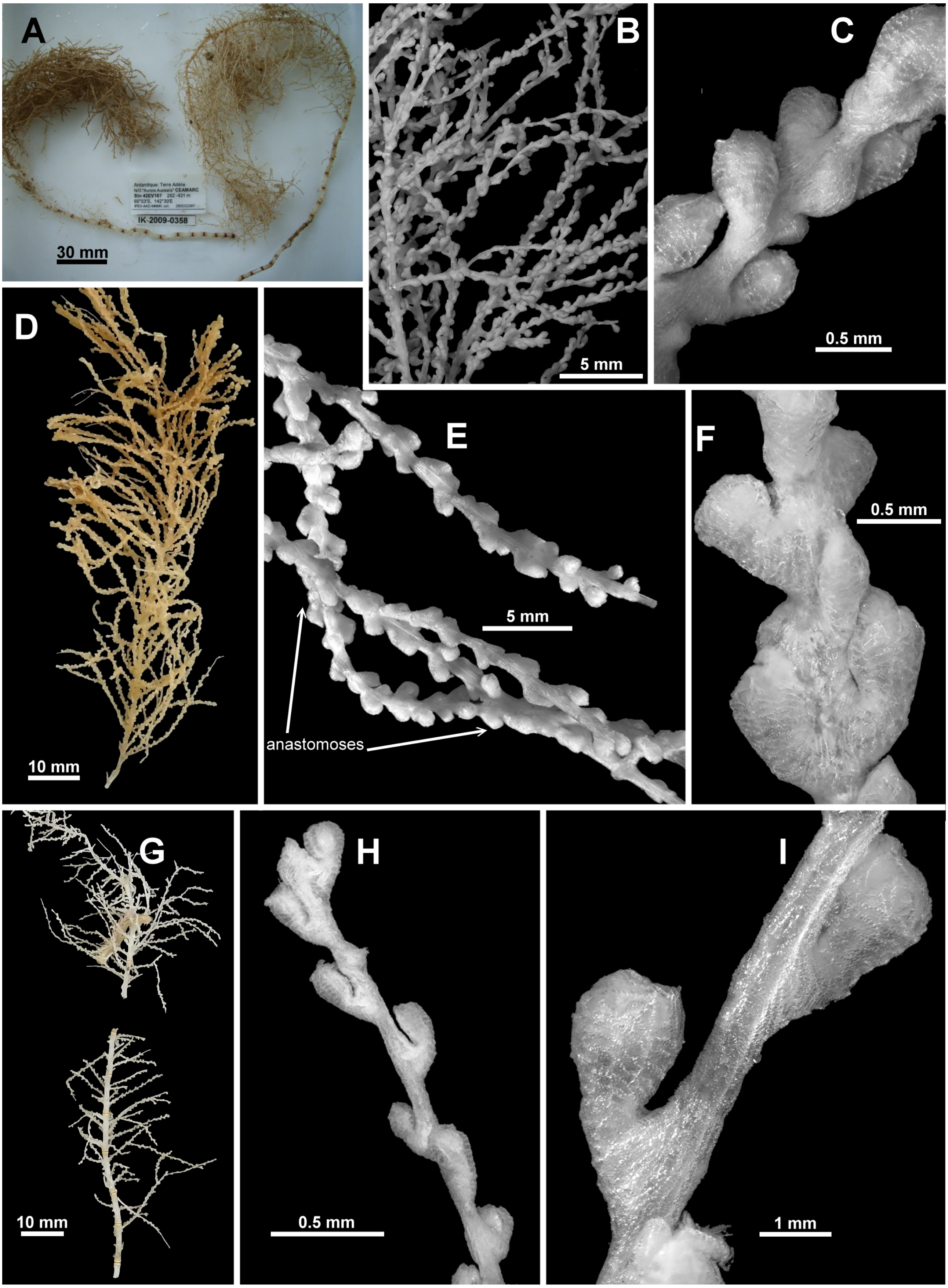

Figure 3.46. *Primnoisis gracilis* (Gravier, 1913): A-C. MNHN IK-2009-358, (A). Colonies; (B). Polyp distribution; (C). Polyps. D-F. TMAG K4301: (D). Colony; (E). Anastomoses; (F). Polyps. G-I. TMAG K4303: (G). Colony; (H). Polyp distribution; (I). Polyp.

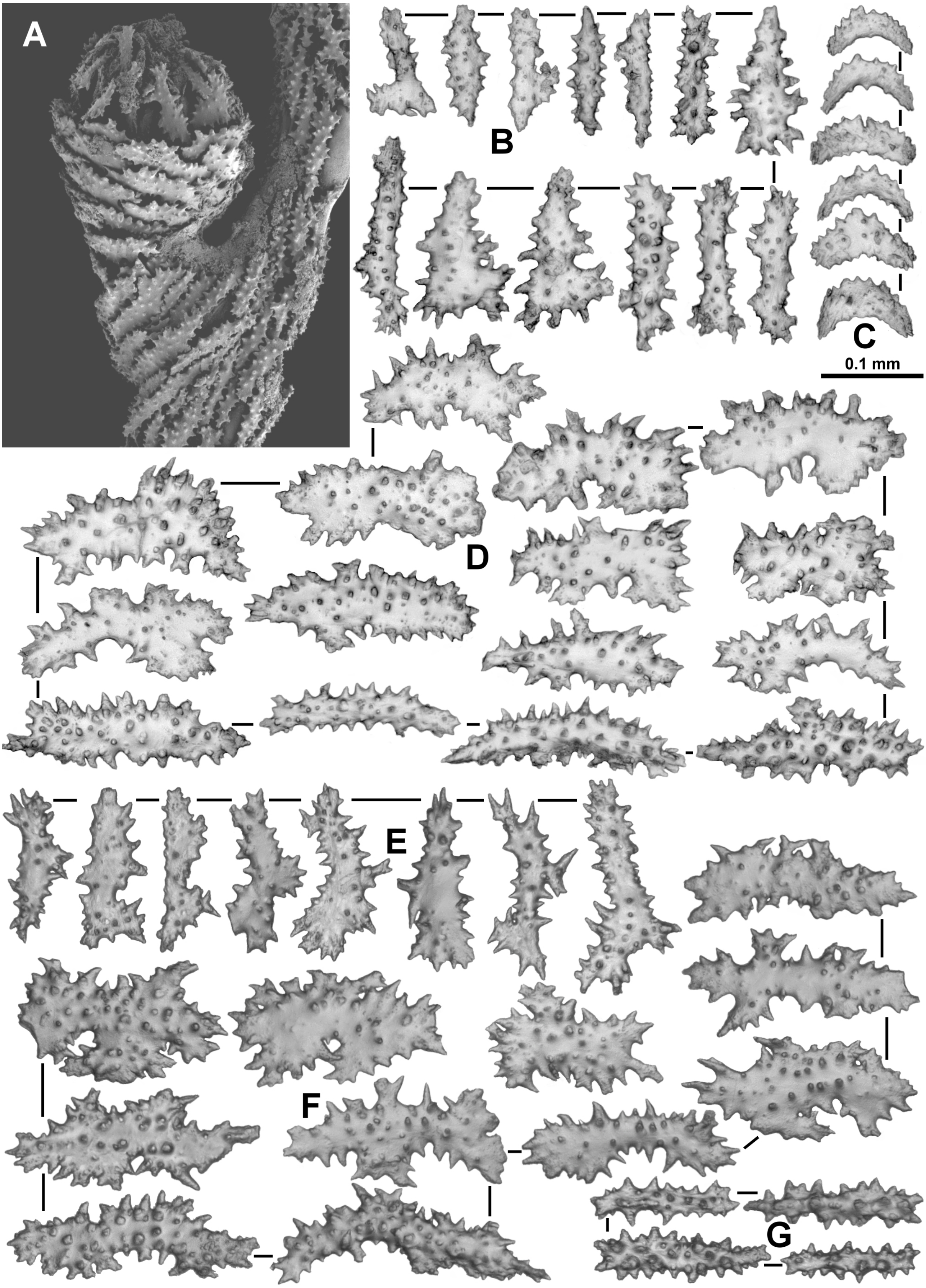

Figure 3.47. *Primnoisis gracilis* (Gravier, 1913): A-D. TMAG K4303: (A). Polyp; (B). Anthopoma sclerites; (C). Tentacle sclerites; (D). Polyp body sclerites. E-G. TMAG K4301, sclerites: (E). Anthopoma; (F). Polyp body; (G). Branch coenenchyme.

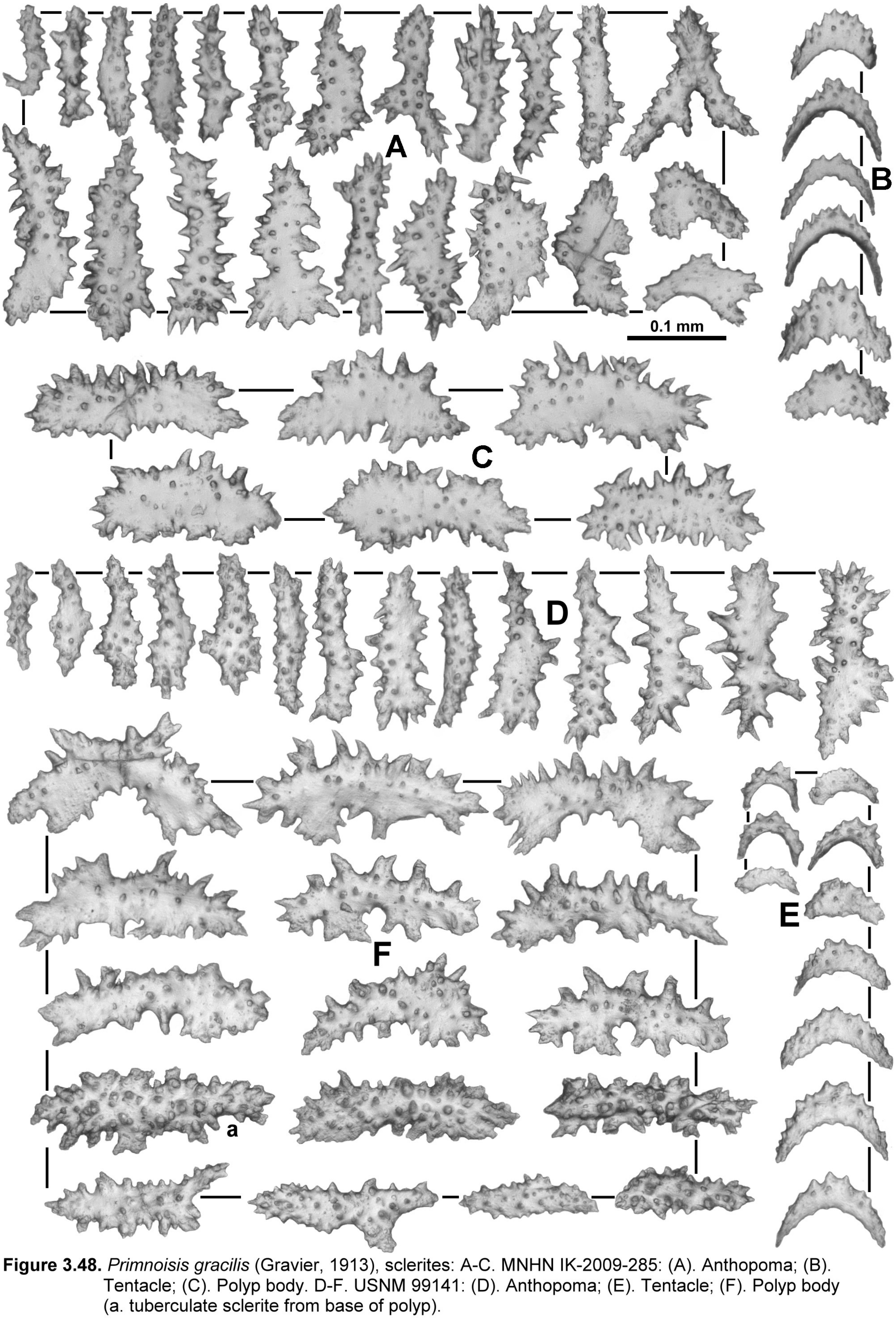

Figure 3.48. *Primnoisis gracilis* (Gravier, 1913), sclerites: A-C. MNHN IK-2009-285: (A). Anthopoma; (B). Tentacle; (C). Polyp body. D-F. USNM 99141: (D). Anthopoma; (E). Tentacle; (F). Polyp body (a. tuberculate sclerite from base of polyp).

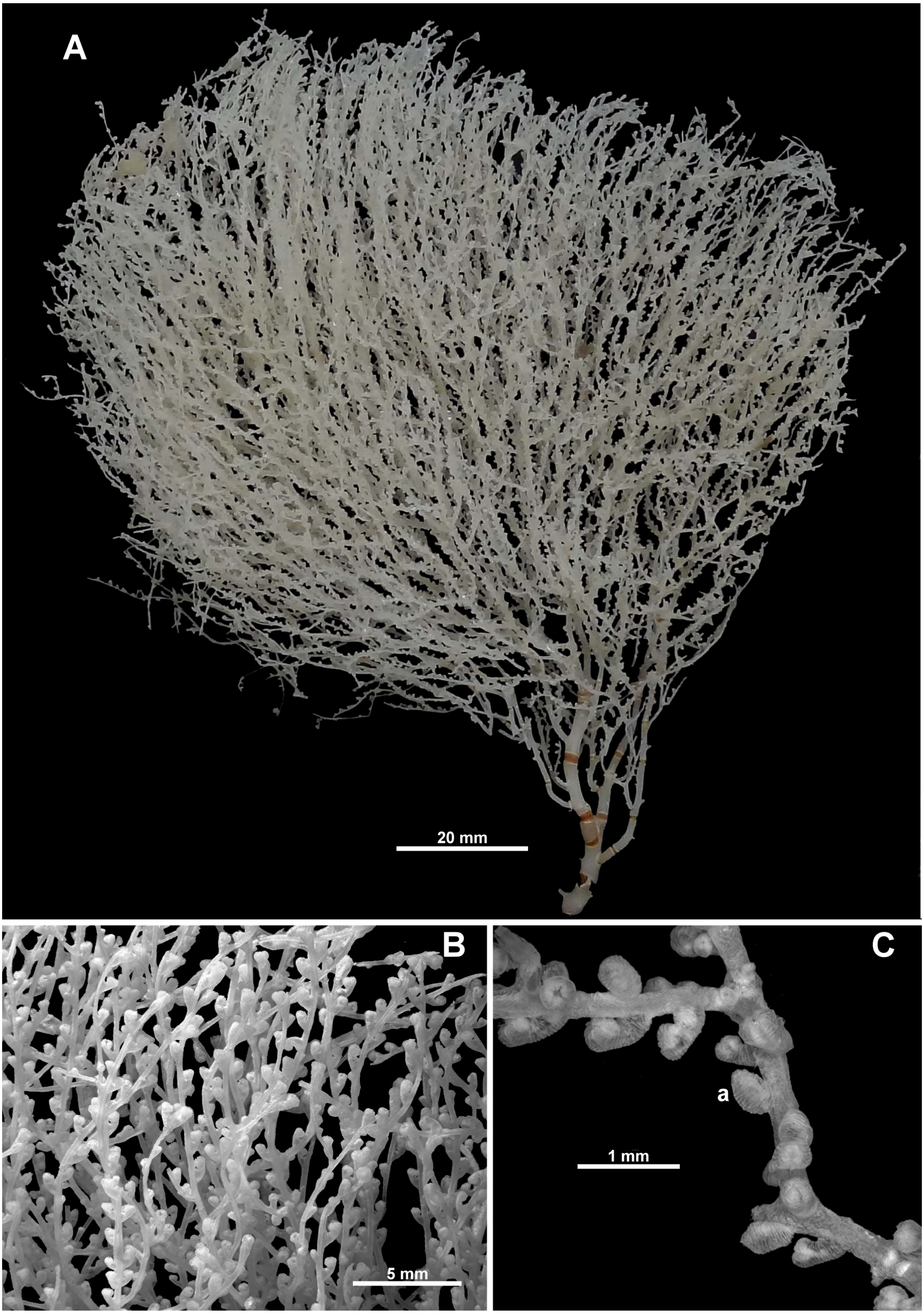

Figure 3.49. *Primnoisis millerae* n. sp., holotype: A. Colony; B. Branching; C. Polyp arrangement (a. brooding polyp).

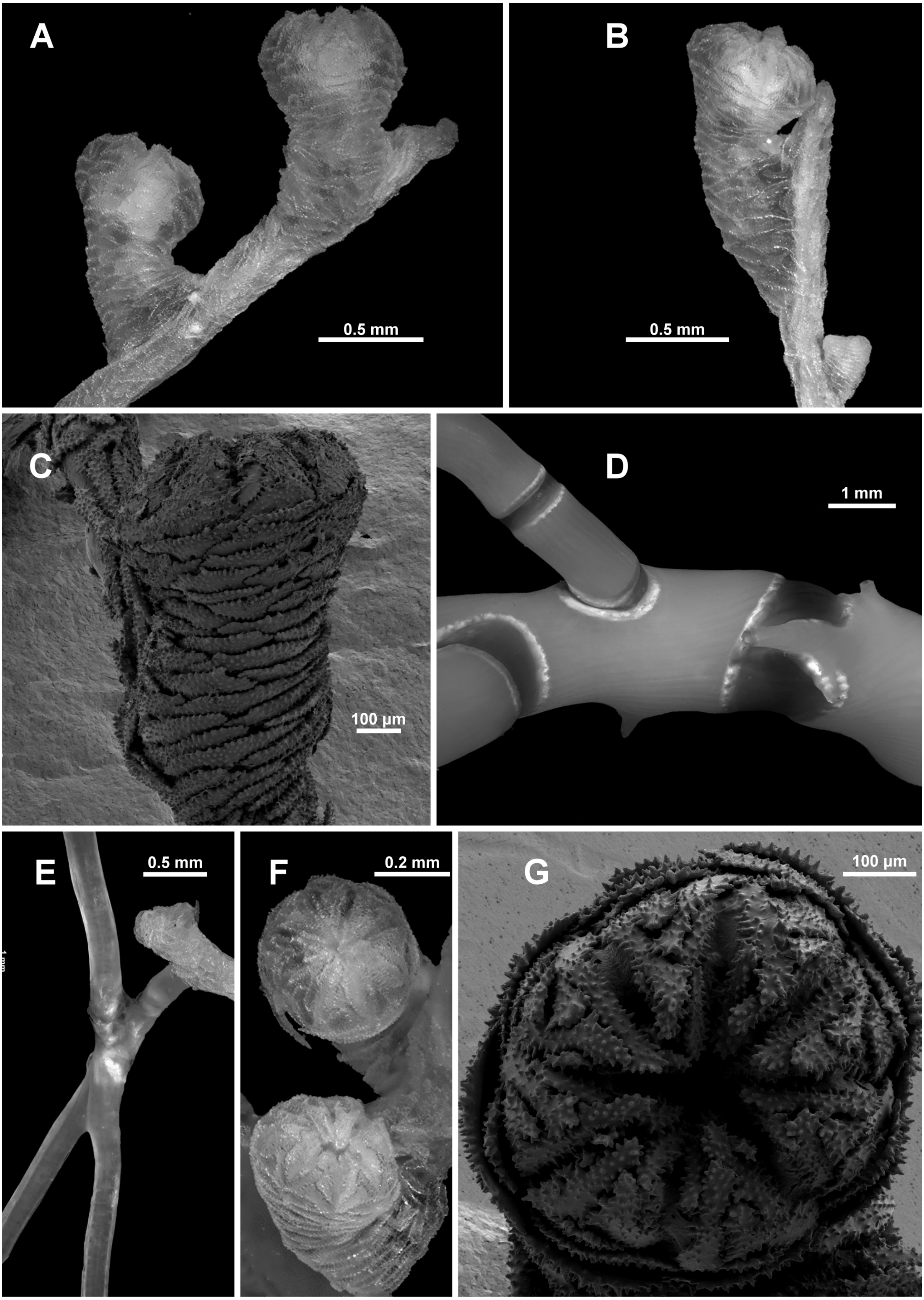

Figure 3.50. *Primnoisis millerae* n. sp., holotype: A-C. Polyps; D. Proximal axis; E. Distal twig with anastomoses; F-G. Anthopomas.

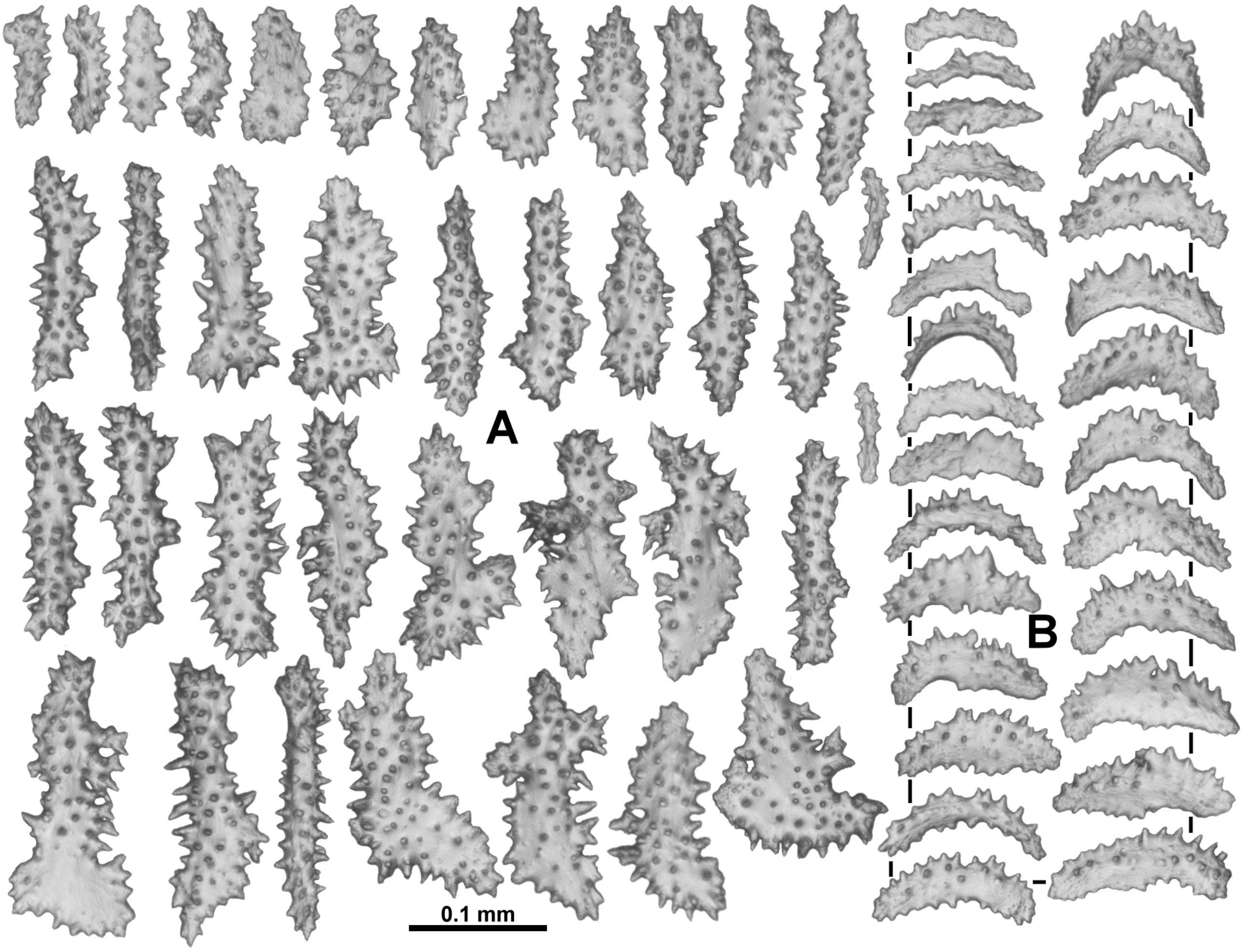

Figure 3.51. *Primnoisis millerae* n. sp., holotype, sclerites: A. Anthopoma; B. Tentacle.

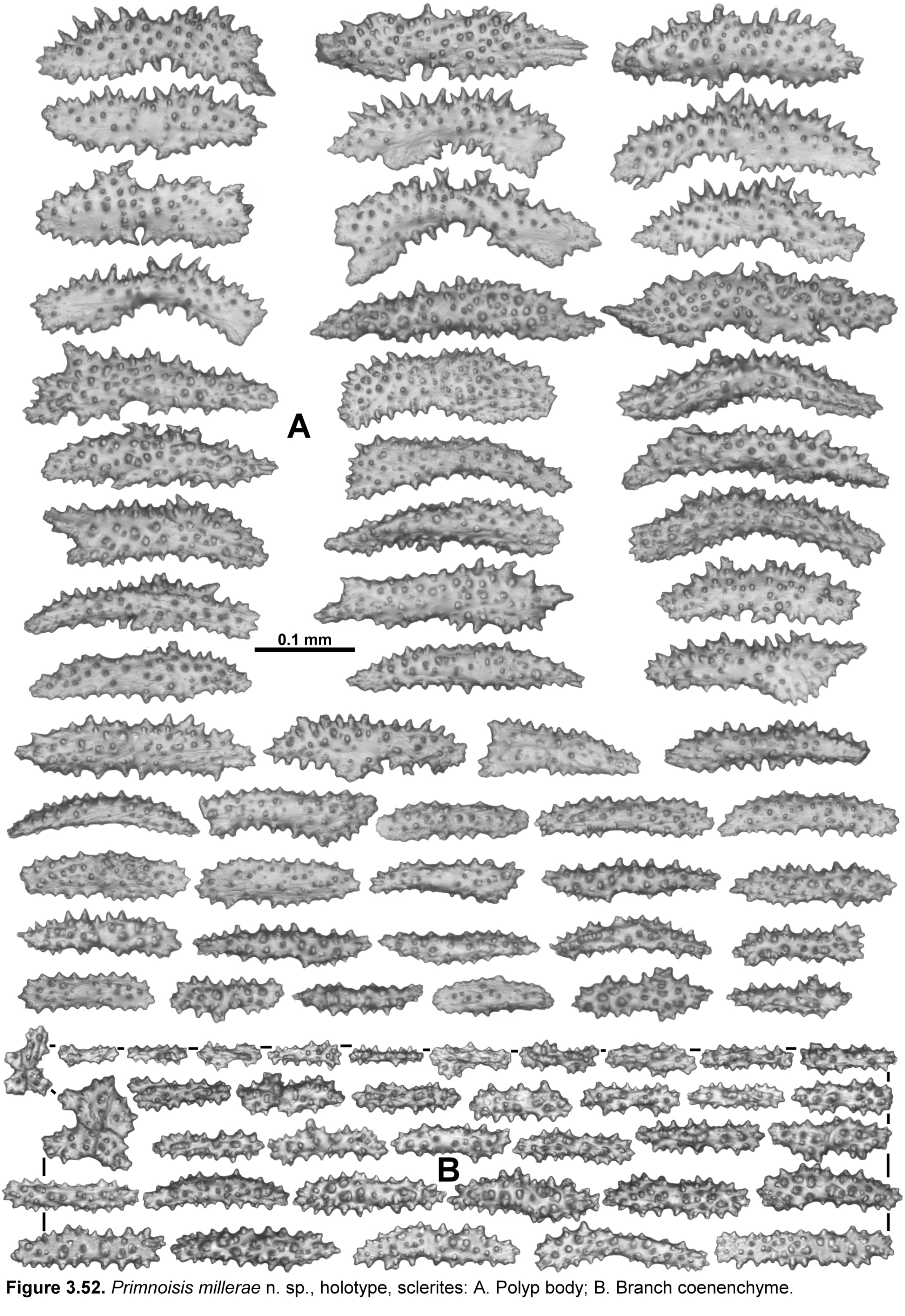

Figure 3.52. *Primnoisis millerae* n. sp., holotype, sclerites: A. Polyp body; B. Branch coenenchyme.

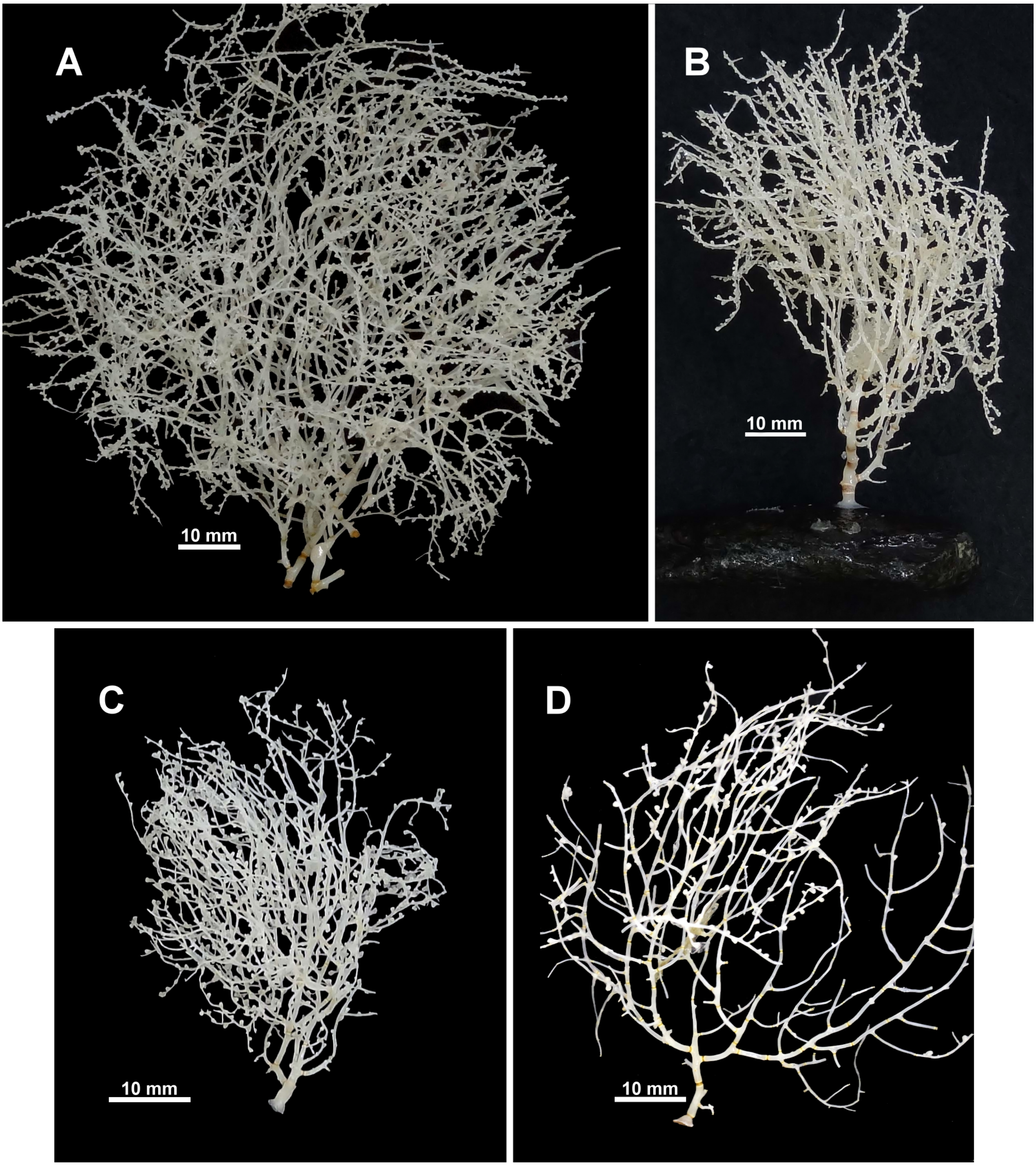

Figure 3.53. *Primnoisis millerae* n. sp.: A. NIWA 65172; B. NIWA 65168; C-D. NIWA 65173, two colonies.

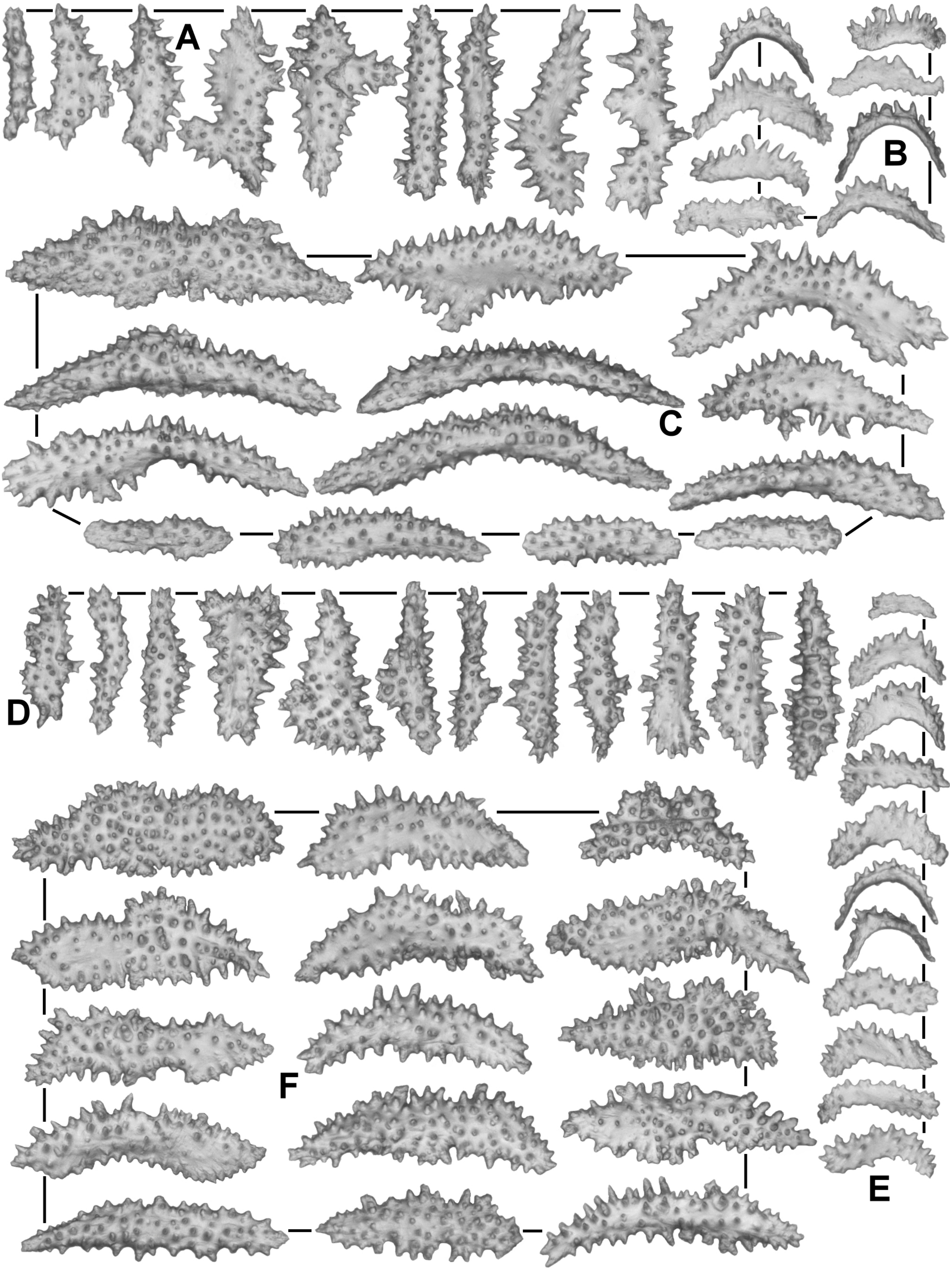

Figure 3.54. *Primnoisis millerae* n. sp., sclerites: A-C. NIWA 65173: (A). Anthopoma; (B). Tentacle; (C). Polyp body. D-F. NIWA 65168: (D). Anthopoma; (E). Tentacle; (F). Polyp body.

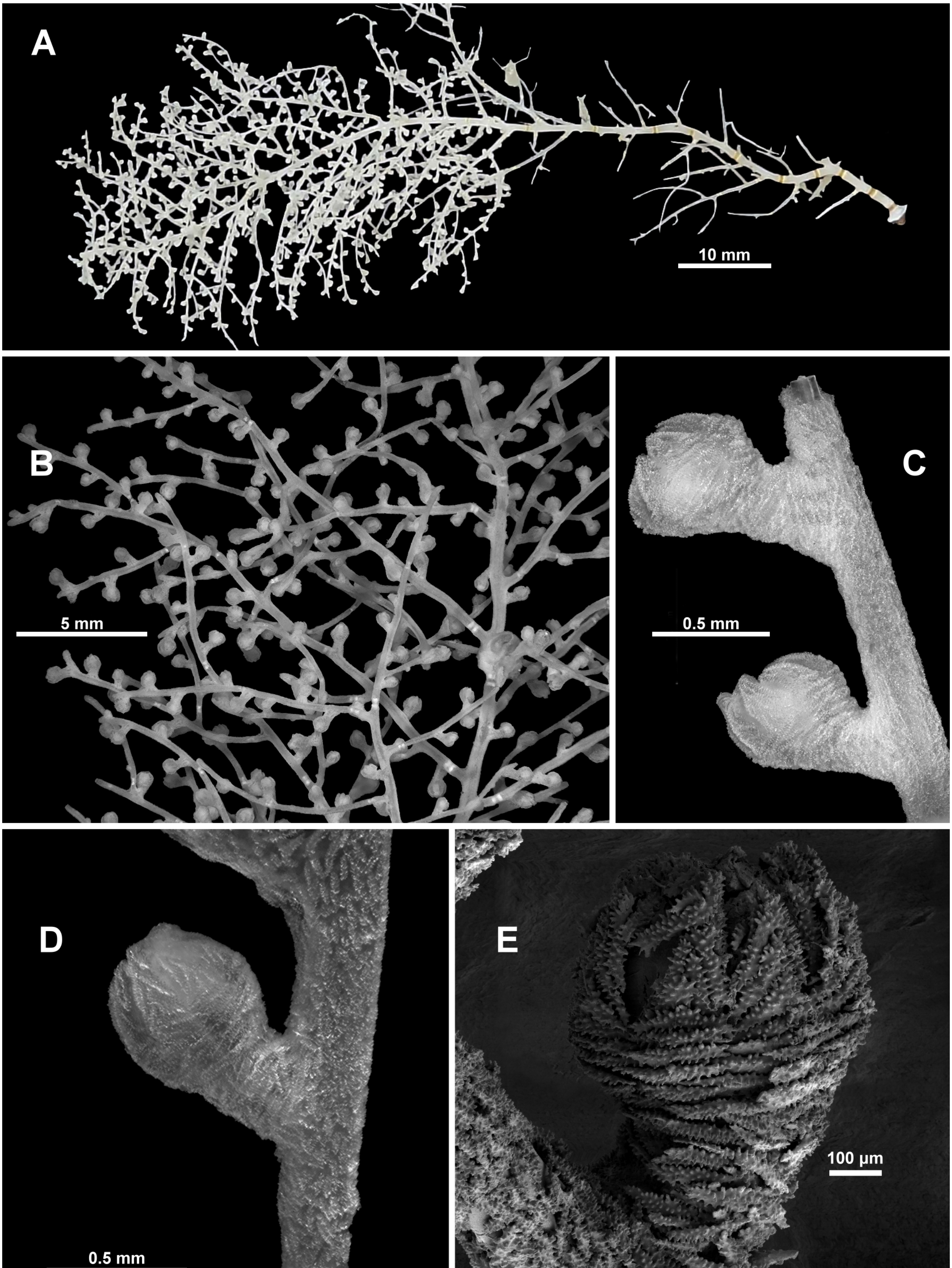

Figure 3.55. *Primnoisis niwa* n. sp, holotype: A. Colony; B. Branching; C-E. Polyps.

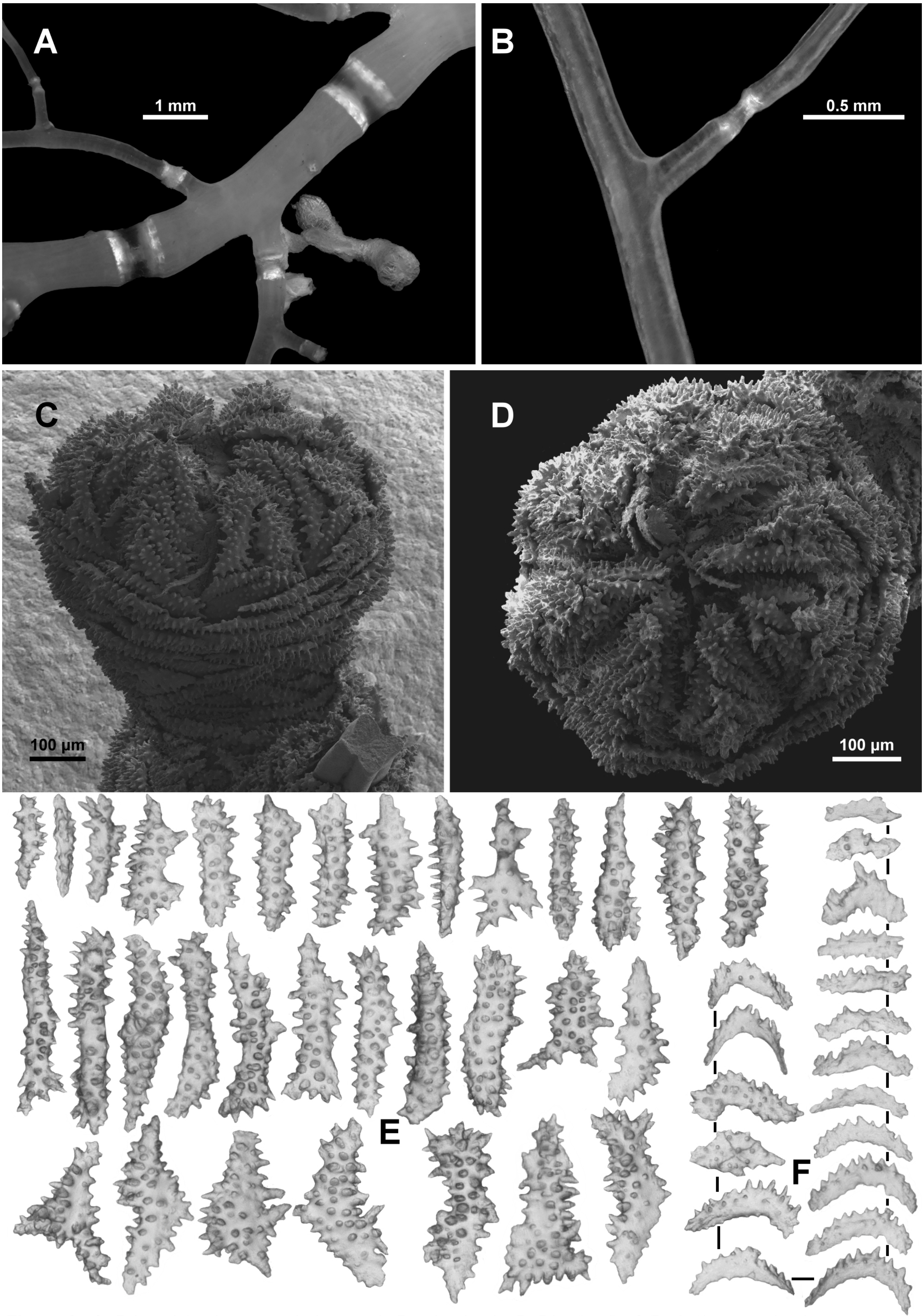

Figure 3.56. *Primnoisis niwa* n. sp, holotype: A. Proximal axis; B. Distal axis; C-D. Anthopoma in place; E. Anthopoma sclerites; F. Tentacle sclerites.

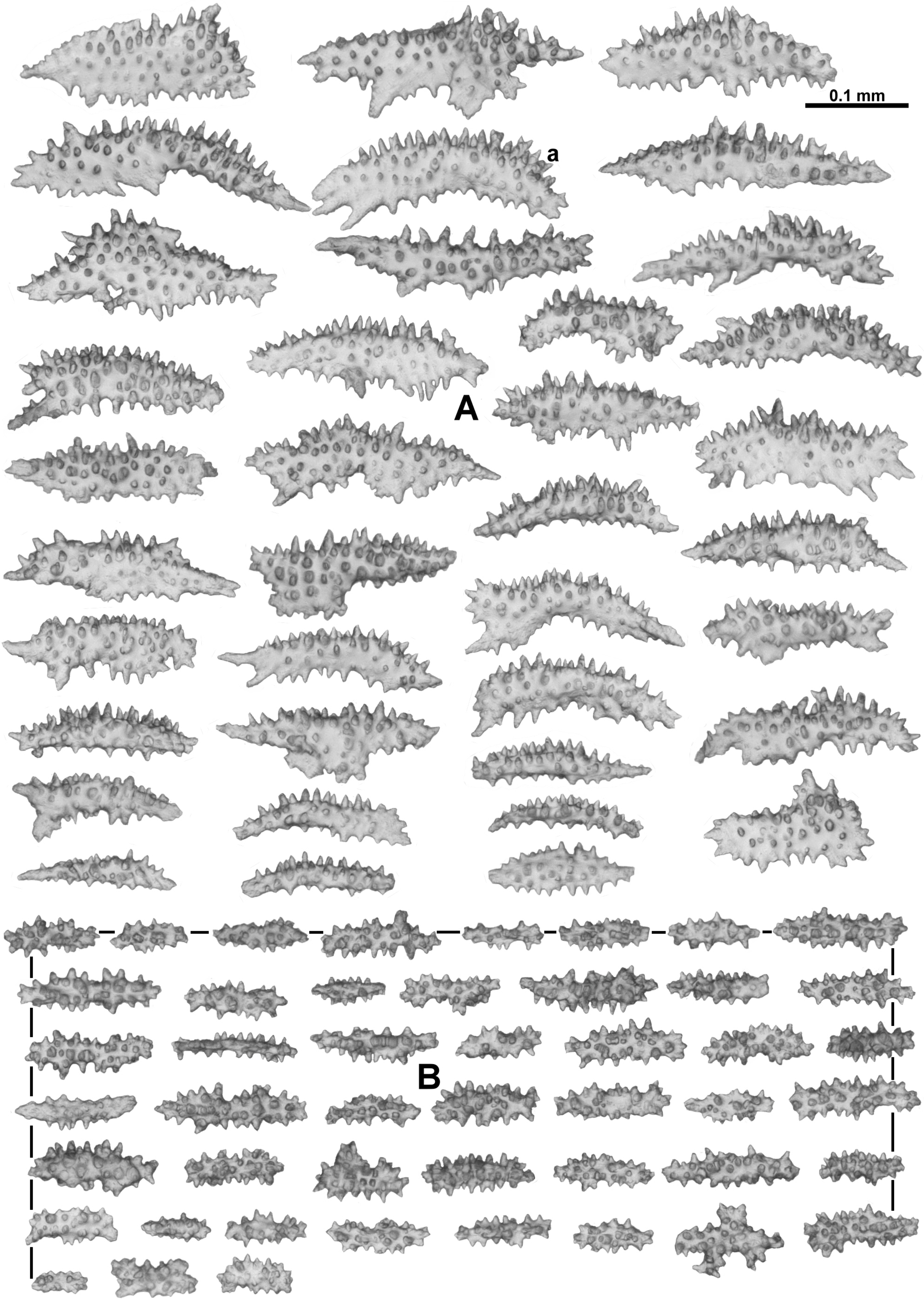

Figure 3.57. *Primnoisis niwa* n. sp, holotype, sclerites: A. Polyp body (a. sclerite with crowded distal margin); B. Branch coenenchyme.

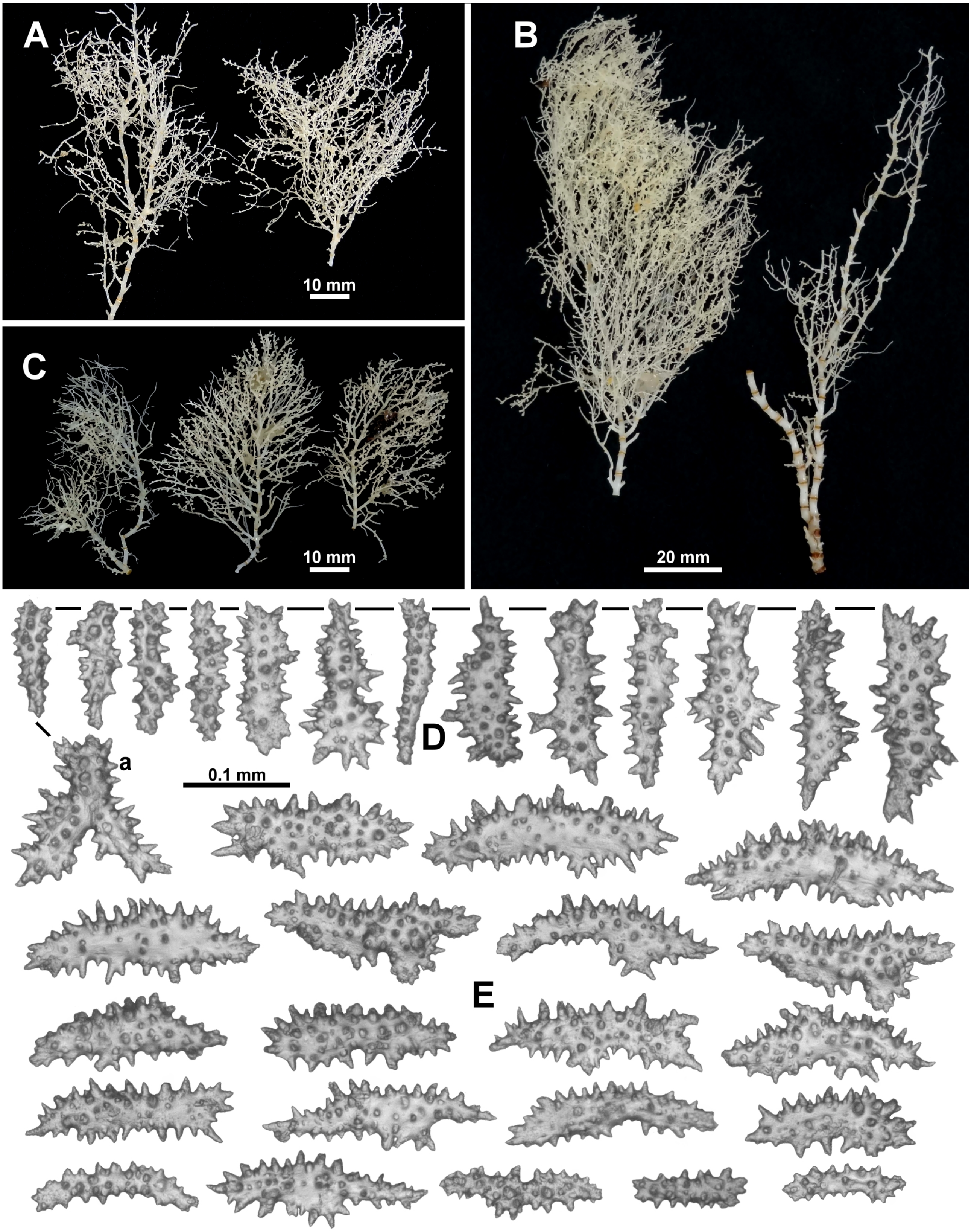

Figure 3.58. *Primnoisis niwa* n. sp.: A. NIWA 40634 lot; B. unregistered AAD sample lot; C-F. NIWA 41002, (C). Colonies; (D). Anthopoma sclerites (a. possible merged sclerite); (E). Polyp body sclerites.

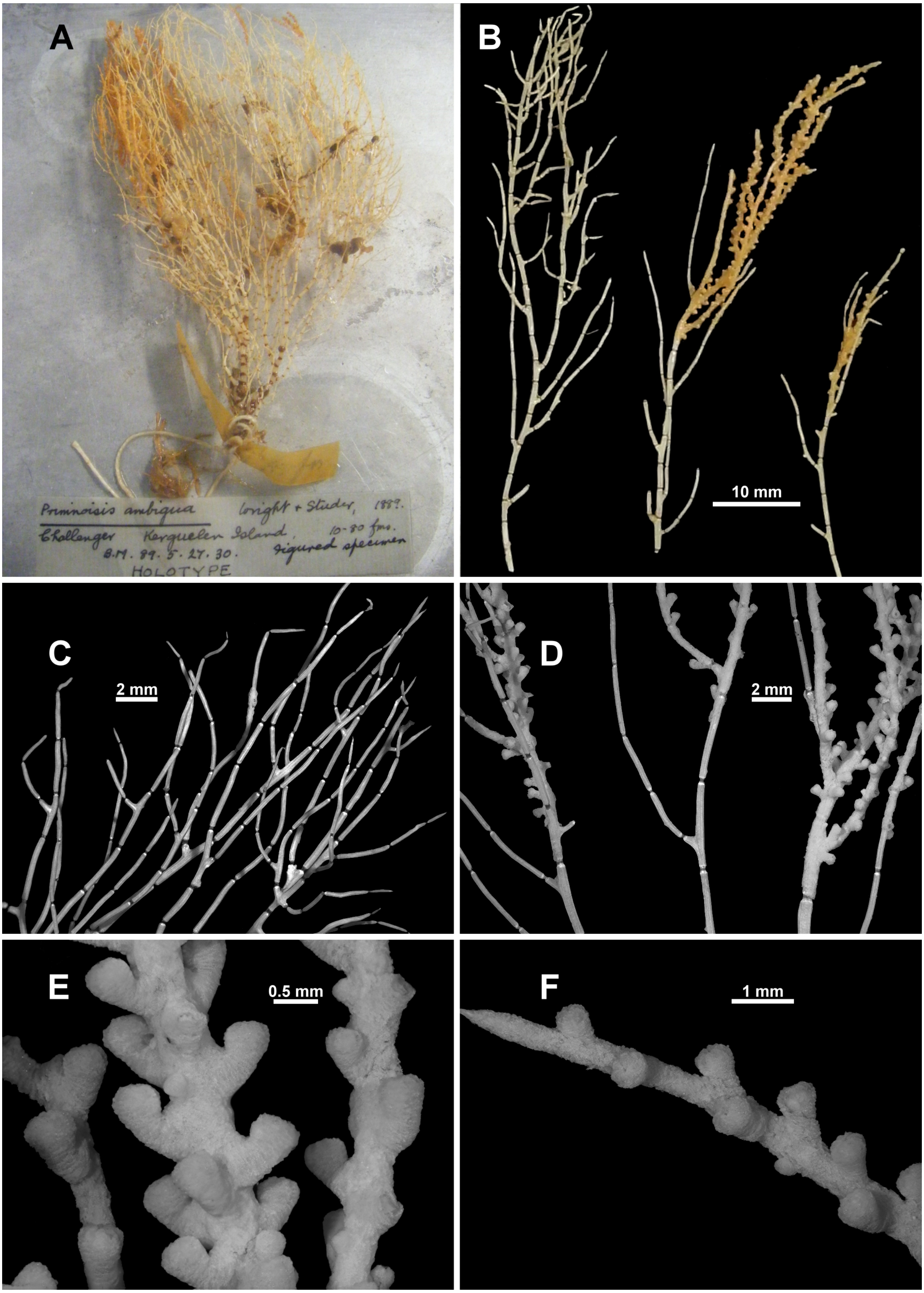

Figure 3.59. *Primnoisis ambigua* Wright & Studer, 1889, holotype: A. Colony; B. Portion examined; C. Distal twigs; D. Branching and polyp arrangement; E. Crowded polyps; F. Polyps on twig tip. (A. Courtesy of NHMUK staff).

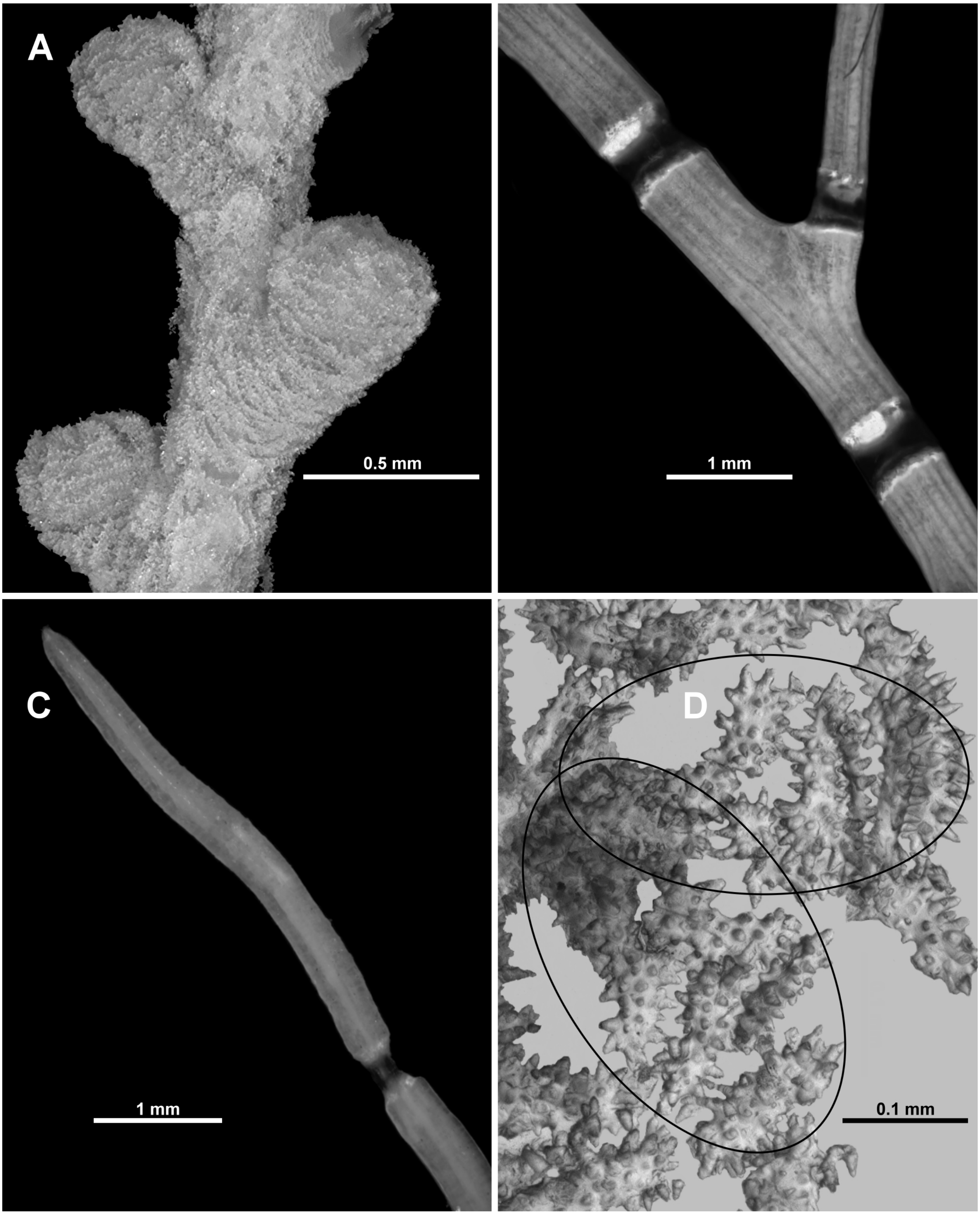

Figure 3.60. *Primnoisis ambigua* Wright & Studer, 1889, holotype: A. Polyp; B. Proximal axis; C. Twig axis; D. Anthopoma sclerites in situ (two octants circled).

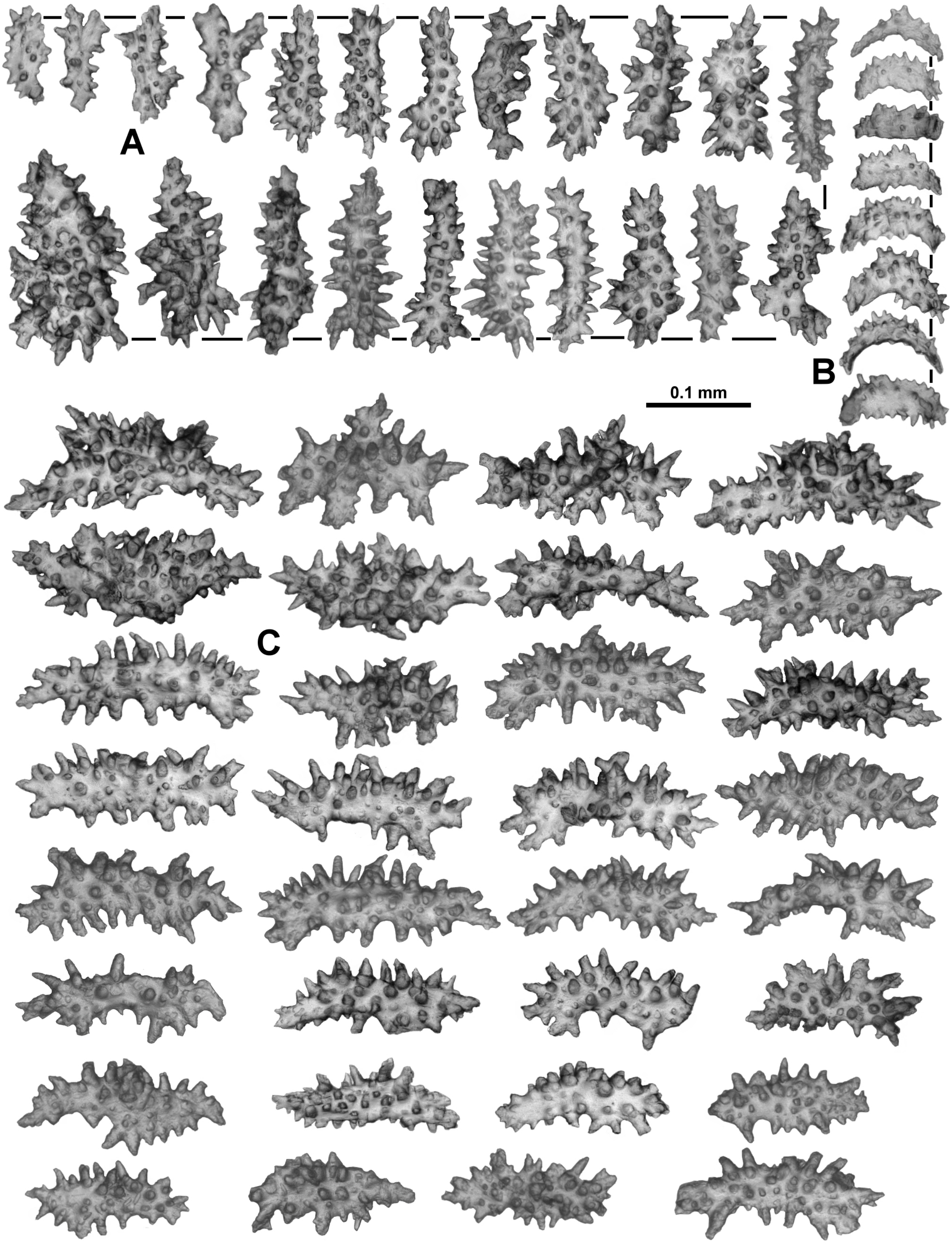

Figure 3.61. *Primnoisis ambigua* Wright & Studer, 1889, holotype, sclerites: A. Anthopoma ; B. Tentacle; C. Polyp body.

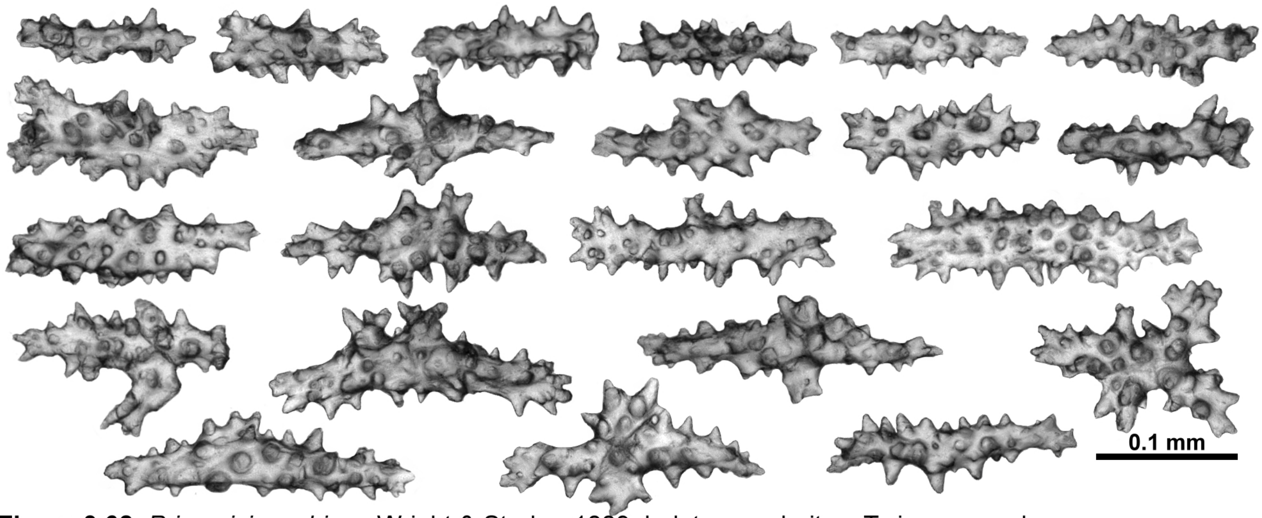

Figure 3.62. *Primnoisis ambigua* Wright & Studer, 1889, holotype, sclerites: Twig coenenchyme.

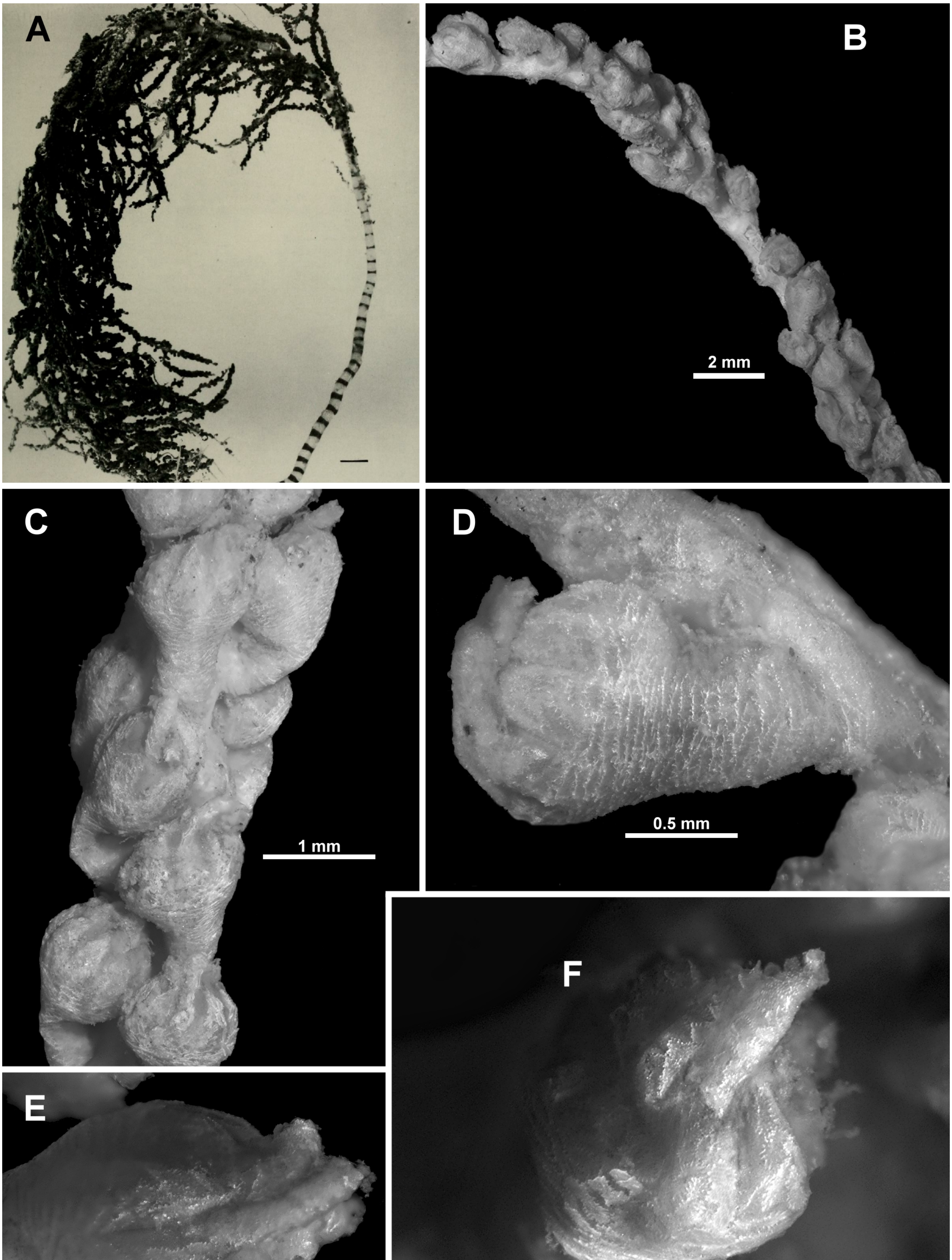

Figure 3.63. *Primnoisis mimas* Bayer & Stefani, 1987, holotype: A. Colony (from Bayer & Stefani 1987, Fig. 5); B. Fragment examined; C-D. Polyps. E. Anthopoma in situ; F. Tentacle sclerites in situ.

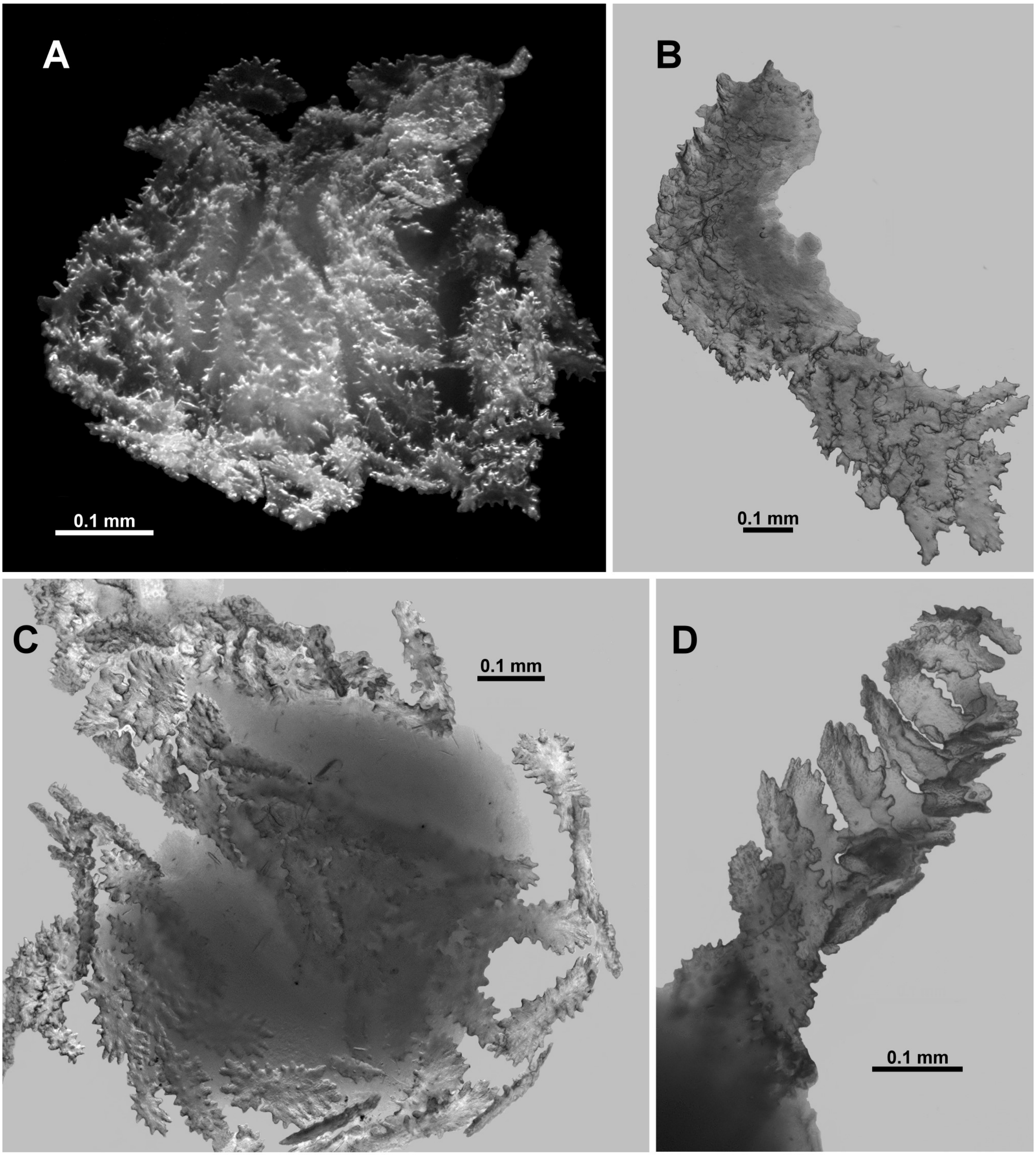

Figure 3.64. *Primnoisis mimas* Bayer & Stefani, 1987, holotype: A. Anthopoma sclerites in situ; B-C. Anthopomal and tentacle sclerites in situ; D. Tentacle sclerites in situ.

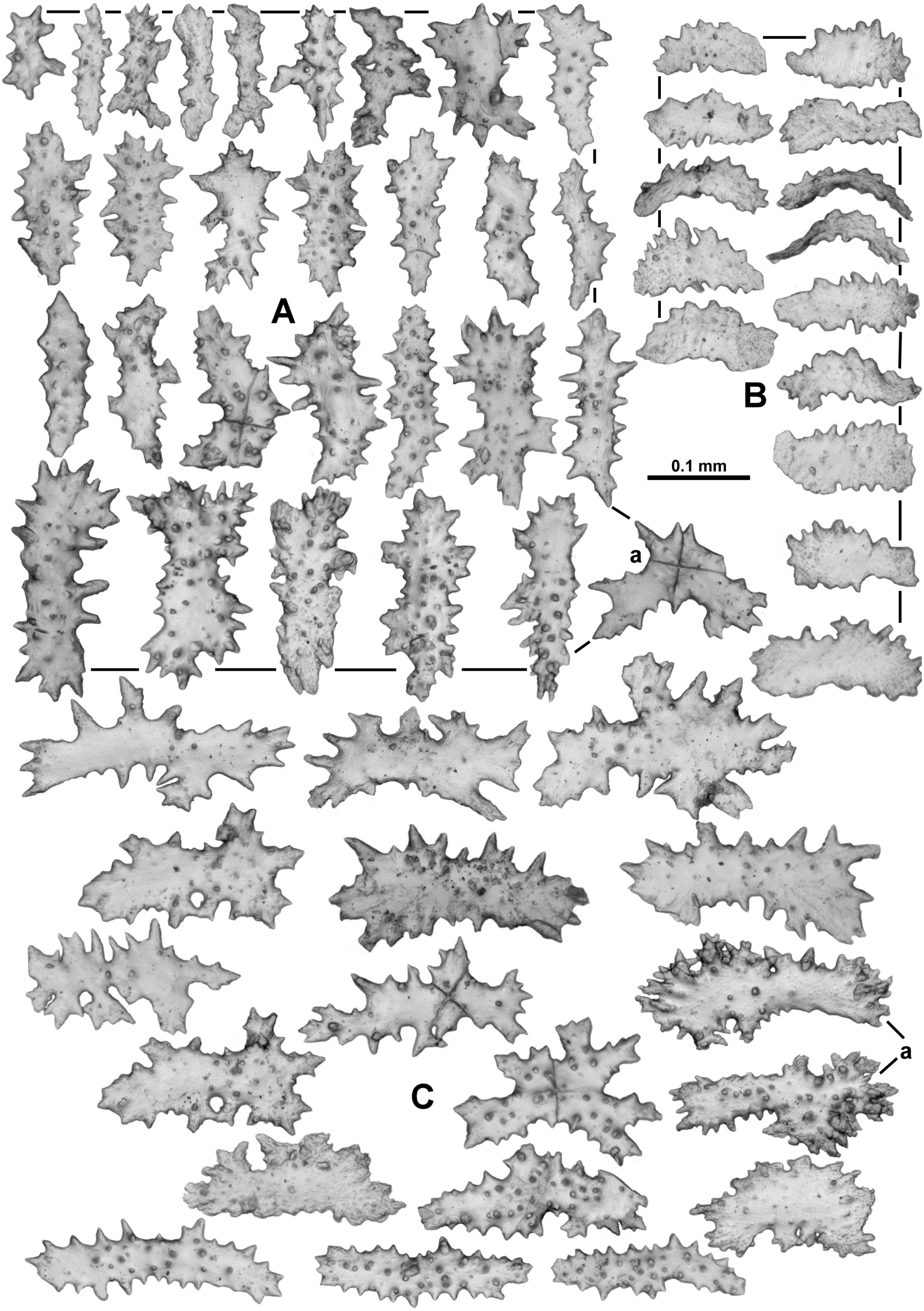

Figure 3.65. *Primnoisis mimas* Bayer & Stefani, 1987, sclerites: A. Anthopoma (a. transitional sclerite); B. Tentacle; C. Polyp body (a. sclerites with complex sections).

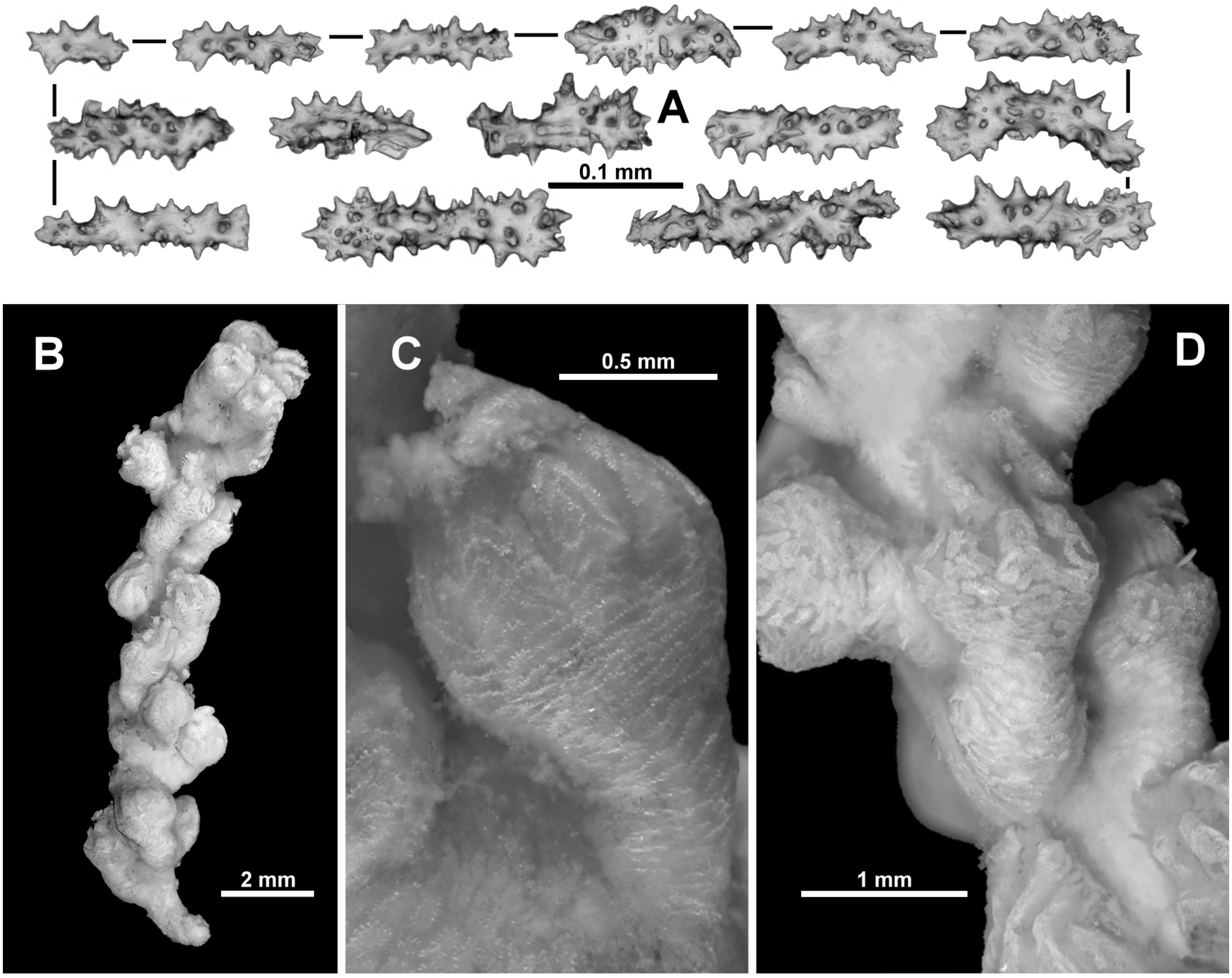

Figure 3.66. *Primnoisis mimas* Bayer & Stefani, 1987: A. Holotype, twig coenenchyme; B-D. Paratype USNM 78537: (B). Fragment; (C-D). Polyps.

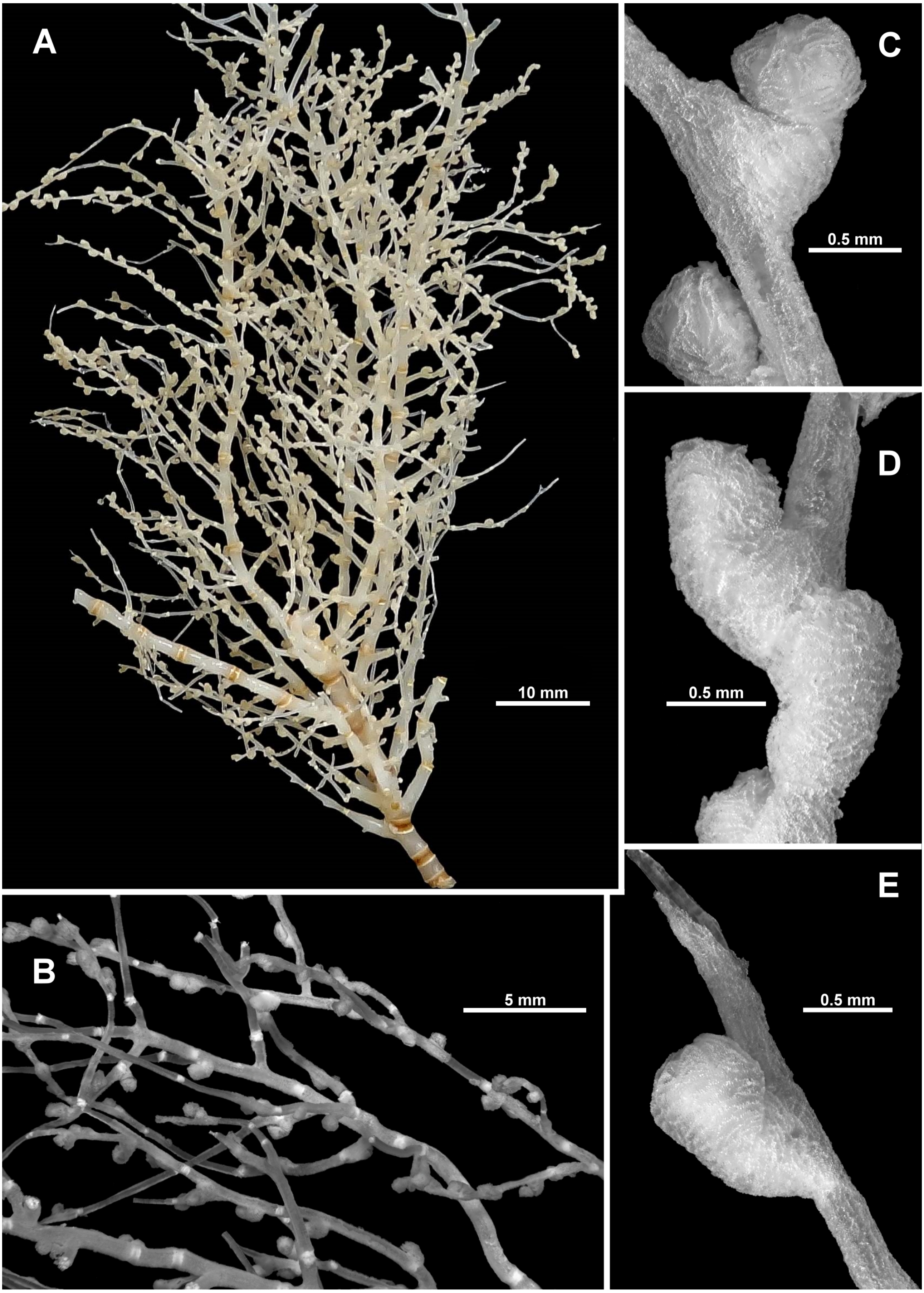

Figure 3.67. *Primnoisis tasmani* n. sp., holotype: A. Colony; B. Branching; C-E. Polyps.

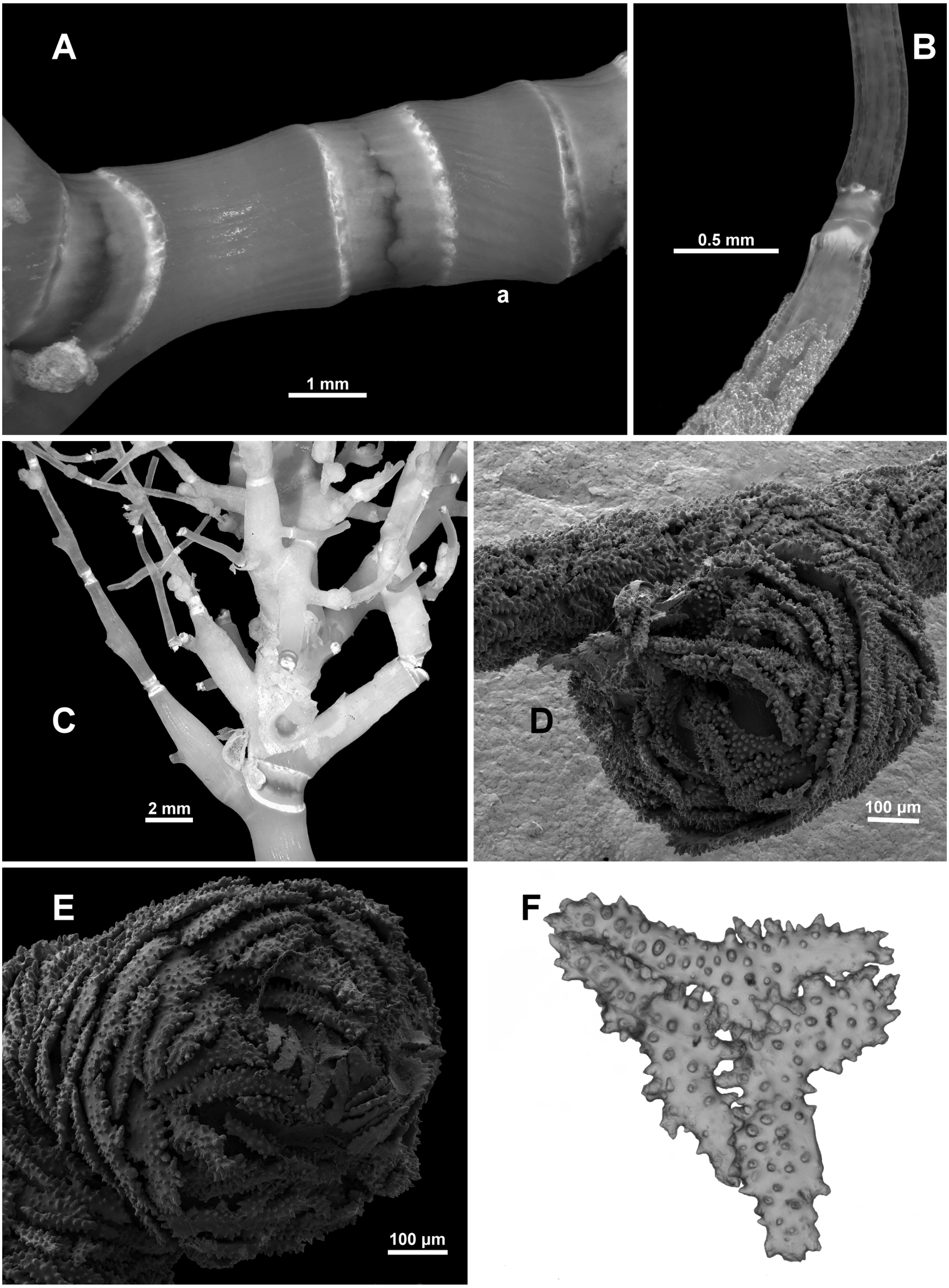

Figure 3.68. *Primnoisis tasmani* n. sp., holotype: A. Proximal axis (a. ridges twisting around the internode); B. Twig axis; C. Swollen internodes; D-E. Anthopomas; D. Proximal part of an octant.

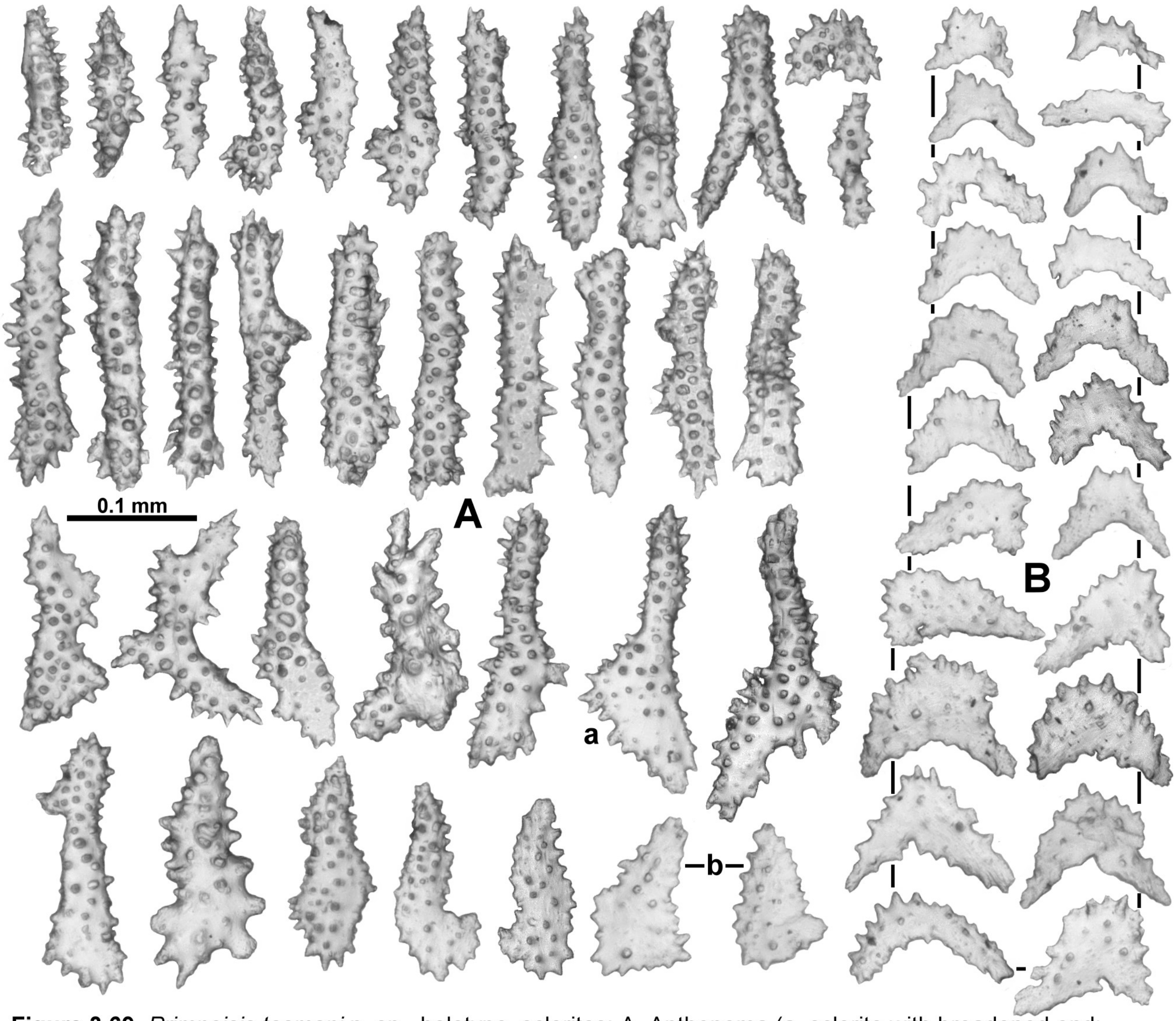

Figure 3.69. *Primnoisis tasmani* n. sp., holotype, sclerites: A. Anthopoma (a. sclerite with broadened end; b. flattened scales); B. Tentacle.

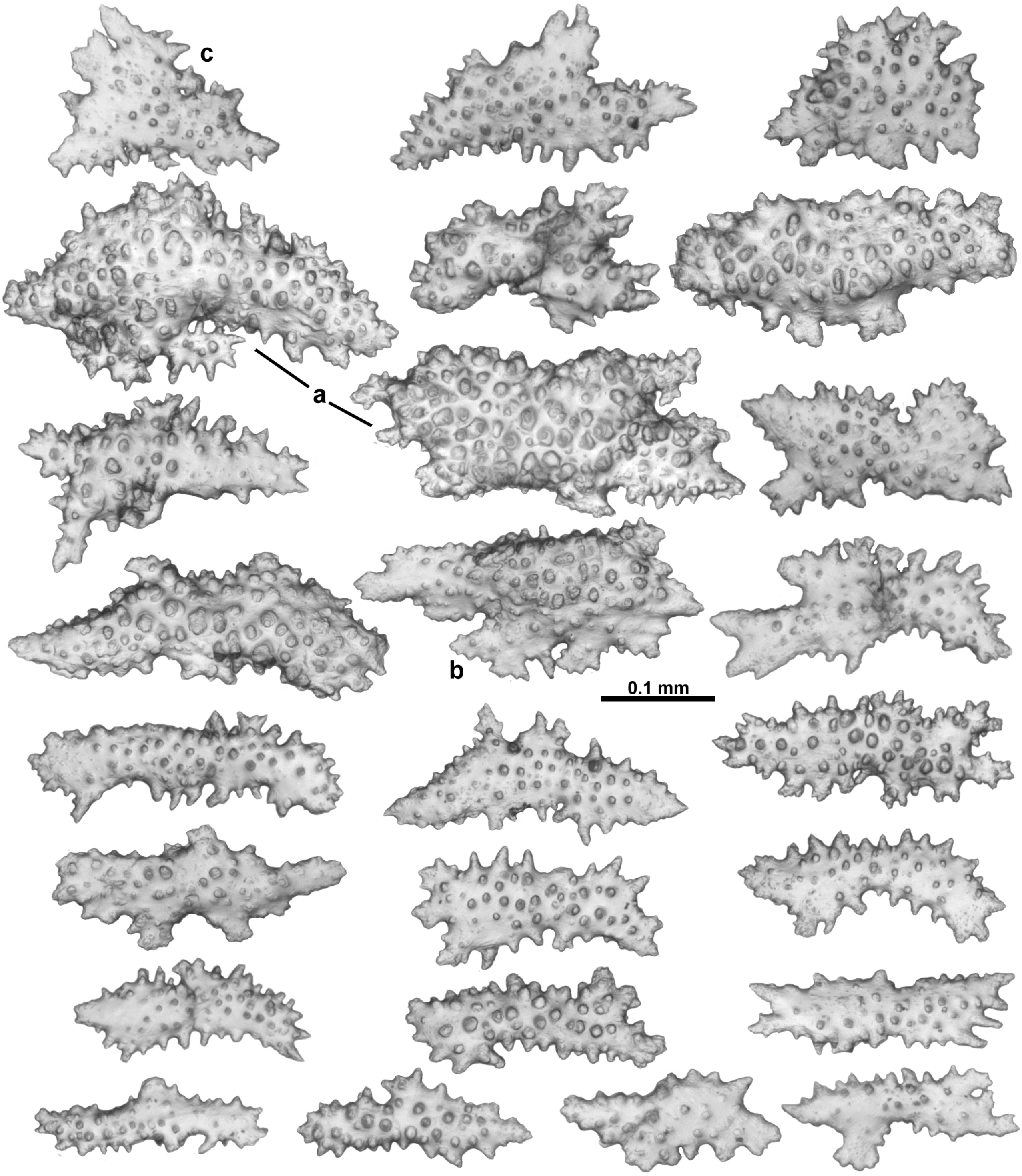

Figure 3.70. *Primnoisis tasmani* n. sp., holotype, sclerites: Polyp body (a. large, bulky sclerites; b. sclerite with root-like processes; c. triangular sclerite).

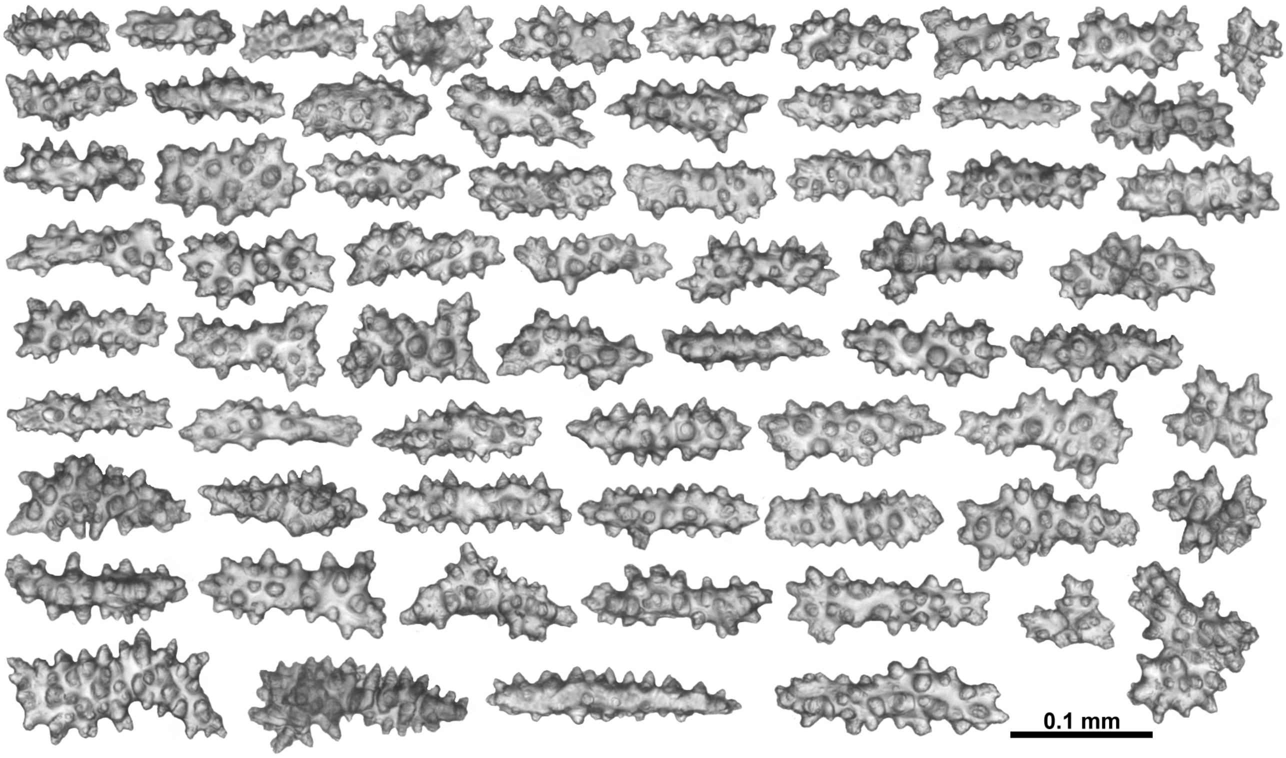

Figure 3.71. *Primnoisis tasmani* n. sp., holotype, sclerites: Branch coenenchyme.

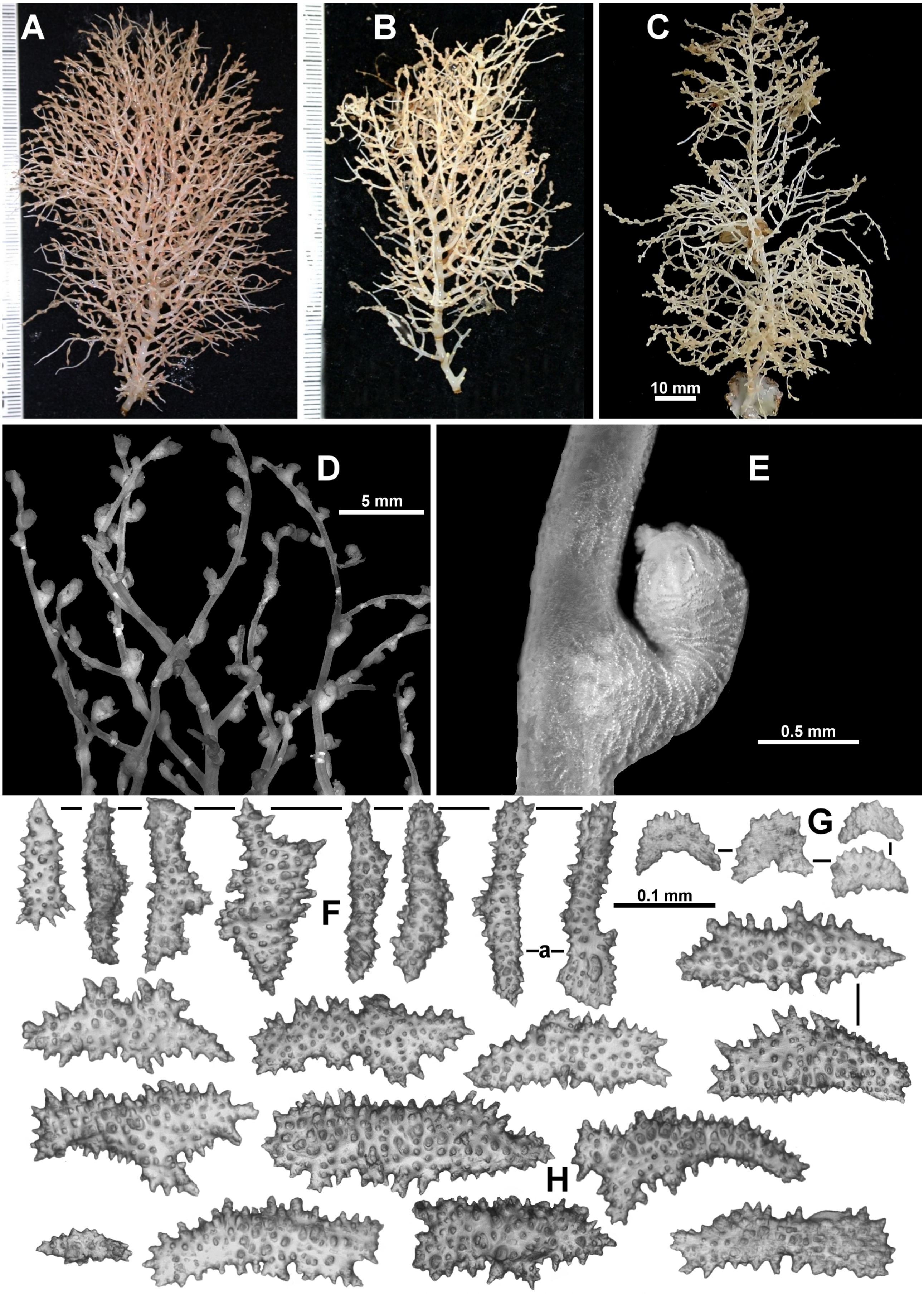

Figure 3.72. *Primnoisis tasmani* n. sp.: A. TMAG K4031; B. TMAG K4029; C. NTM CO12684; D-E. TMAG K4031: (D). Distal twigs; (E). Polyp. F-H. NTM CO12684 sclerites: (F). Anthopoma (a. tuberculate rods); (G). Tentacle; (H). Polyp body. (A, B. Courtesy of Karen Gowlett-Holmes, CMAR).

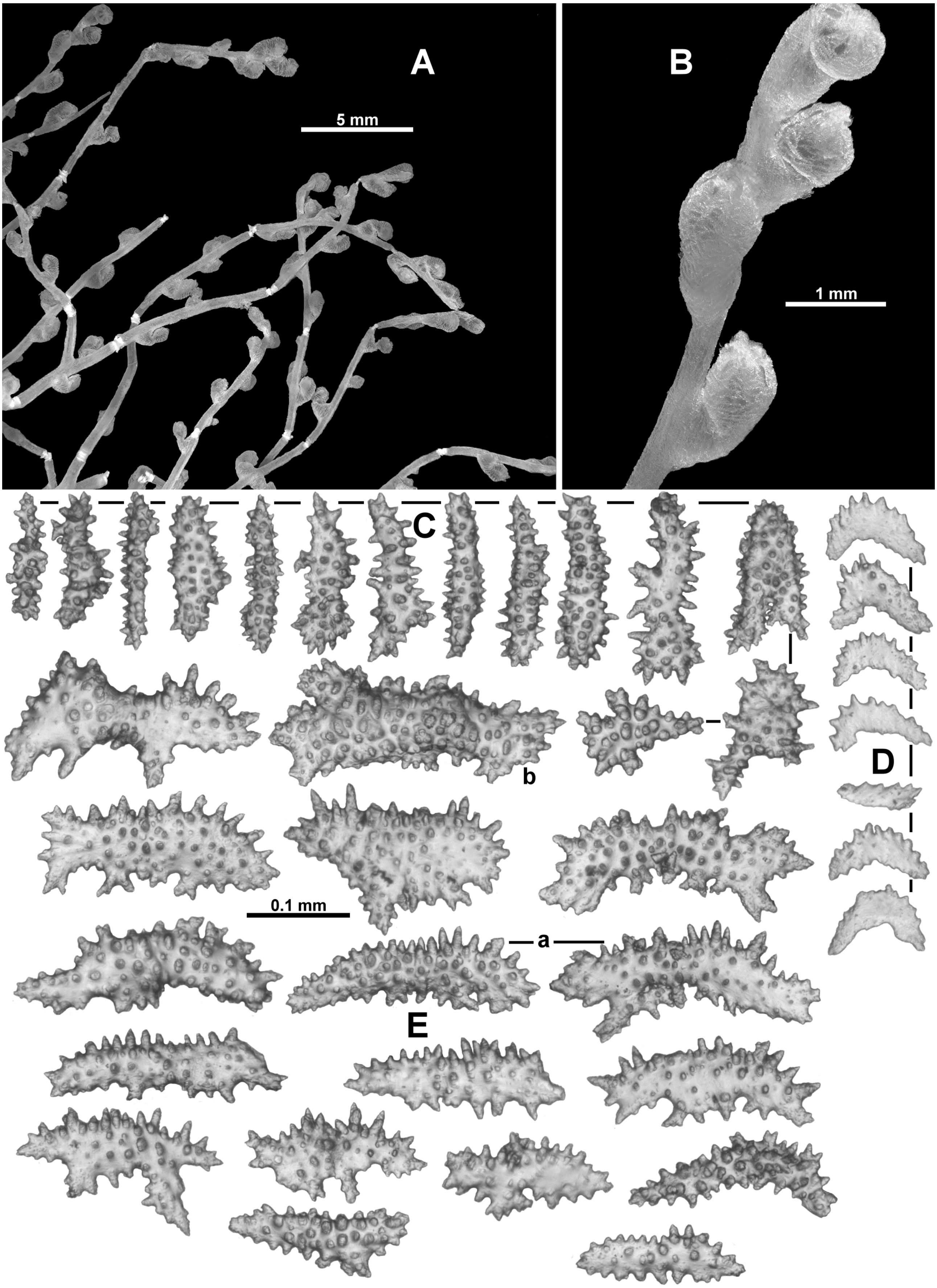

Figure 3.73. *Primnoisis tasmani* n. sp., TMAG K4278: A. Polyp arrangement; B. Polyp; C. Anthopomal sclerites; D. Tentacle sclerites; E. Polyp body sclerites (a. sclerites with pronounced spines on distal margin; b. large, bulky sclerite).

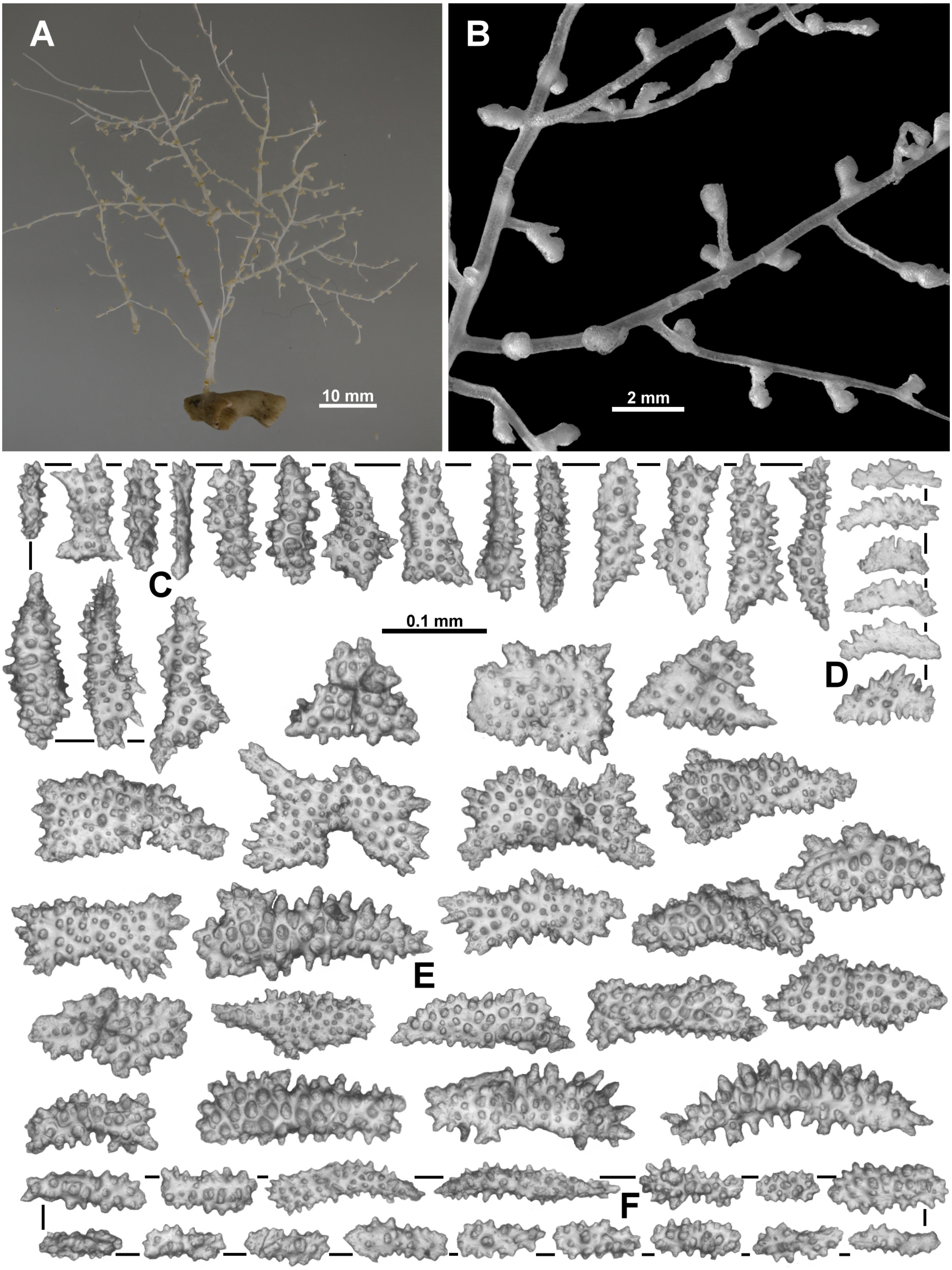

Figure 3.74. *Primnoisis tasmani* n. sp., TMAG K4283: A. Colony; B. Polyp arrangement; C. Anthopomal sclerites D. Tentacle sclerites; E. Polyp body sclerites; F. Coenenchyme sclerites.